UNIVERSITY OF ALBERTA

FOREPAW PREFERENCE IN THE *MACACA ARCTOIDEA*; EFFECTS OF TEST CHARACTERISTICS

by

© ROBERT LYLE BARTON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF PSYCHOLOGY

EDMONTON, ALBERTA

SPRING, 1972

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Forepaw Preference in the Macaca Arctoidea: Effects of Test Characteristics" submitted by Robert Lyle Barton in partial fulfillment of the requirements for the degree of Master of Science.

Abstract

A series of 17 tests was administered to 10 *Macaca arctoidea* to examine the effect of task characteristics on the production of forepaw preferences. The series of tests was divided into three experiments. The task characteristics were divided into two main categories: Incentive (I) measures or forepaw used to obtain the incentive and Manipulation (M) measures or forepaw used to manipulate the manipulanda. In addition, a judgement of overall task complexity was considered in evaluating the production of forepaw preferences. Complexity was defined as the degree of involvement of three manipulative features in a task: movement of manipulanda, simultaneous use of both forepaws and chaining of responses. Usually the moveable manipulanda and the simultaneous use of forepaws features were confounded.

Those tasks which were more complex produced the stronger forepaw preferences. There was also an indication that the I and the M task characteristics differentiated laterality preference; there was a bias to the left on the I measures and to the right on the M measures.

ACKNOWLEDGEMENTS

I particularly wish to thank Dr. Charles Beck for his continuing support and guidance during my work on this thesis.

I also wish to thank Charles Richmond for his assistance in producing the photographs for the thesis.

I am deeply indebted to my wife Susanne for her patience and understanding during my work on this manuscript.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

GENERAL INTRODUCTION

Interest in laterality of human hand preference has a long history. References to handedness are frequent in religious and superstitious beliefs; these references usually imply superiority of the right hand. For example, the right hand is specified for benediction in Genesis XLVIII:14 while in the same verse the left hand is mentioned as a secondary choice. In Psalms there are many references to the power of the right hand (Psalms XVI:8, Psalms XX:6, Psalms CIX:1) but there are no references to the power of the left hand. In superstitious beliefs left handedness was commonly associated with being unlucky and with warlocks and witches.

Aristotle and Plato noted that people preferentially used one hand or the other and proposed theories about the origins of the difference. Aristotle (Wile, 1934) claimed that the organs of the right side of the body were more powerful than those of the left. This suggestion was influential and held prominance for many years. Plato stated that the hand preferred was determined by the way a baby was carried in the arm of a nurse because of the restriction this caused in the use of one arm (Wile, 1934). As pointed out by Baldwin (1906) this theory would predict approximately equal numbers of left and right handed people in the population depending upon whether the nurse was left or right handed. Plato's theory was not as influential as Aristotle's because observations on the population did not uphold it.

After Aristotle's demise it was a long time before other authors became interested in the origin of handedness. Sir Thomas Browne (Wilkin, 1852), in 1648, stated that right handedness is only a convention and that "Dextral pre-eminence has no regular or certain root in nature [p.3]". Sir Thomas Carlyle (Froude, 1884) suggested that the question about the origin of handedness was not worth asking but felt that hand preference probably developed from fighting because it was important to protect the heart and therefore the shield was carried in the left hand.

In 1886 Sir Daniel Wilson argued that dexterity should be tracable to some speciality of organic structure (Wilson, 1886). He agreed somewhat with Aristotle's position that the organs on the right side of the body were stronger but in additon felt that the left side of the brain was dominant.

Most of the work discussed above was based on personal observation. Only relatively recently have quantitative tests been developed to measure handedness in humans. These tests consist of recording responses on such manual tasks as throwing a ball, hammering, writing, gripping a dynamometer, etc. Rife (1922) argued that these tasks are essentially unimanual and that bimanual tasks such as using a shovel, an axe, a broom, a bat, etc., should be included in tests of handedness. Sir Daniel Wilson (1886) had already looked at the use of an axe by Canadians and assumed that

the preferred hand is placed near the axe head. Rife (1922) suggested that the hand "nearer the business end of the instrument [p.475]" is the preferred hand for the operation. This agrees with Sir Wilson's assumption.

The problem of deciding what produces the greatest degree of consistent hand preferences or simply what are the best measures of hand preference has produced disagreement among authorities. Aristotle is quoted in the first English encyclopedia (Pedro, 1613) as mentioning that handedness is manifested in non-standard activities. Woo, in 1928, stated that the hand dynamometer gave a good indication of hand preference and that steadiness in holding a rod was another good indicator. Haefner (1929) stated that ball throwing is the best indicator of handedness and argued that bimanual tasks are less signficant indicators of handedness than are uni-manual tasks. More recently Sir Cyril Burt (1961) has stated that the preferred hand is the hand executing the most delicate actions in a task. Presently there is general agreement that tasks involving precise manipulations give a good indication of hand preference.

Estimations of the numbers of people with left hand preference vary considerably. One often quoted statistic occurs in the Bible in Judges 20:16. This states that the tribe of Benjamin had 700 left handed men from a total of 26,000, a percentage of 2.7. More recent estimations

vary between two percent of the population to 30 percent (Baldwin, 1911; Wile, 1932). The variation in the estimates arises largely from methodological differences in determining handedness. Methods as various as noting which hand threw a stick, the number of left hand writers at elementary schools and which hand carried an umbrella or suitcase were used in obtaining these figures. The average percentage obtained from large populations is about five percent (Ballard, 1911; Gordon, 1921; Ogle, 1871).

Although there is some disagreement about specifics there is general agreement that hand preference exists in humans. The next section reviews the literature on laterality or forepaw preference in some subhuman species.

Forepaw preference in subhuman species:

Quantitative data on forepaw preferences in subhuman species are lacking prior to 1900 and not much was done in this area until about 1930. Unsupported statements that forepaw preference was not present were made by anthropologists like Brinton (1896). He argued that anthropoids and other primates are ambidextrous. A similar argument is made by Woodruff (1902): "None of the anthropoids, indeed no other animal except man, shows any preference in the use of either a right or a left limb. They are all ambidexterous (or ambisinistrous) [p.120]."

Degree of forepaw preference:

Kounin (1938) argued that forepaw preference may be present in monkeys and investigated this possibility with a battery of four tests: three tests of manual preference and one test of visual preference. The subjects of his experiment were three rhesus monkeys, three cebus monkeys and one spider monkey.

All the manual tasks involved the use of only one forepaw. For the first test, Handedness I, the subject (S) had to reach for an incentive through a hole in the floor of the cage. Kounin (1938) recorded the number of times each forepaw was used in obtaining the reward. In the second test, Handedness II, the S had to open the cover of a box and hold it open while obtaining the reward. Only one forepaw could be used in this operation and Kounin recorded the number of times each forepaw was used. The third test, Handedness III, involved a S's use of a rake to pull a reward object toward itself. The forepaw used to manipulate the rake was the one recorded. Kounin's fourth test, Eyedness Test, involved the S looking through a hollow tube. He recorded which eye was used to look through the tube.

Kounin's (1938) results demonstrated that the first two tests, Handedness I and II, produced a greater degree of forepaw preference than did the third test, Handedness III.

However, it should be noted that he calculated his mean percentage preferences across species, that is, he grouped together rhesus, cebus and speder monkeys, obtaining mean percentage preferences for Handedness I and II of 97.6% and 97.7%, respectively compared to a mean percentage preference of 87.8% for Handedness III. Examination of the data grouped between species indicates that the three rhesus monkeys demonstrated mean percentage preferences of 95.6%, 81.8% and 82.6% on Handedness I, II and III, respectively. The three cebus monkeys demonstrated mean percentage preferences of 100%, 99.5% and 94.1% on Handedness I, II and III, respectively. The groups are too small to compare statistically but it appears that the cebus monkeys display stronger preferences and that Handedness I and II possibly elicit stronger preferences. Kounin suggested that Handedness I and II were more reliable than Handedness III and that they possessed a greater diagnostic value in differentiating hand preference although he presented no statistics to validate this suggestion. Kounin found that the results of his fourth test, the Eyedness Test, did not necessarily correspond with the results of the handedness tests.

Kounin (1938) concluded from his experiment that the degree of preferential handedness depended on the nature of the task performed, and that those tasks requiring delicate and coordinated manipulations produced the stronger preferences.

Harlow, Settlage and Grether (unpublished, quoted in Kounin, 1938) obtained similar results using two java monkeys, five rhesus monkeys and one pigtail monkey as Ss. They used a battery of three tests in their investigation of forepaw preferences. For their first test the S had to reach through a pipe to obtain an incentive. In the second test the S obtained the incentive from a food cup in front of the cage. For the last test the S pulled a string to which food was attached.

From their results they found that the pipe test produced the highest mean percentage preference of 88.5%. The string test produced the lowest mean percentage preference of 73.3%, while the cup test produced a mean percentage preference of 76.0%.

Referring to his own experiment and to the one by Harlow, et. al., Kounin (1938) concluded that:

> "The results of both experiments strongly suggest the advisability of speaking rather (sic) of degree than of a unit characteristic of handedness in monkeys.... This degree of handedness is greatly determined by the nature of the tests used [p.389]."

Cole (1957) found that a complex task produced greater preferences than a simple task for five *Macaca nemistrina* monkeys. He compared performance on a simple task involving the Ss obtaining an incentive from a flat

tray in front of their cage to performance on a more complex task that invoved the S opening a match box drawer by pulling on a knob and then obtaining the reward. Both tasks could be performed using only one forepaw.

Warren (1958) reported increased forepaw preference on complex tasks in an investigation involving 31 cats and 17 rhesus monkeys. He used a series of three tests. One of the tests involved having the Ss reach for an incentive placed on a wooden tray. The other two tests involved the S displacing a cover to obtain the incentive from a food well underneath. He found that there was a higher proportion of animals displaying significant preferences for one forepaw or the other on the more complex displacement tasks.

Brookshire and Warren (1962) also investigated lateral preferences of 19 rhesus monkeys but reported results which conflict with the ones described above on the effect of increased task complexity. They used six tests in their investigation: three designed to produce unimanual responses and three designed to allow bimanual responses. The three unimanual tasks were:

1. Reach - the S was to remove the incentive from the surface of a tray.
2. Wire - the S was to remove the incentive from a horizontal wire which was pointed toward the test cage.
3. Bottle - the S was to remove the incentive from a vertical transparent bottle three inches high and two inches in diameter

The incentive was clearly visible in each case and the forepaw used to obtain the incentive was recorded on each trial.

The "potentially" bimanual tasks they used were:

1. Hasp - the incentive was partially concealed by a hasp. The hasp could not be lifted more than 0.75 inches, therefore it had to be held in an elevated position while the incentive was extracted. Although it was possible to hold the hasp and obtain the incentive with one forepaw most Ss used two. Performance was scored in terms of the forepaw used in manipulating the hasp and the forepaw used in removing the incentive.

2. Handle box - the incentive was placed in a wooden box five inches square by three inches deep. The box weighed 300 grams. A handle 0.5 inches in diameter and five inches long was attached to the front. When presented to the S the handle was four inches away from the front of the cage, therefore the box was nine inches away. The S had to pull the box toward the cage to obtain the incentive. There were two potentially distinct manipulations involved - the hand used to pull the manipulanda and the hand used to obtain the incentive.

3. Block - the incentive was concealed in a food well covered by a wooden block 10 centimeters square by two centimeters thick. The S was required to displace the block covering the food well on each trial. Performance was scored in terms of the forepaw used to manipulate the block and that used to obtain the incentive.

Brookshire and Warren (1962) conclude:

> "Several investigators have suggested that tasks which require greater manipulative skill elicit stronger hand preferences than simple tasks (Cole, 1957; Kounin, 1938; Warren, 1958). The results of this study render the correlation suspect. The intuitively simple Reach task evoked stronger preferences than were observed on five of six measures of bimanual preference [p.226]".

It should be noted that among the bimanual tasks only the Hasp test elicited predominantly bimanual performance. Unimanual responses were predominant on the other two "potentially" bimanual tasks. Although the Reach task did evoke somewhat stronger preferences than the Hasp test, the difference was minimal. Two Ss had non-significant preferences on the Reach task while three Ss on one measure of the Hasp task (the manipulation) did not reach significance and five Ss on the other measure (incentive) did not reach significance. However, about three times as many trials were given on the Reach task than on the Hasp tasks, therefore smaller deviations on the former task were significant. Also, as demonstrated by Warren (1958), practice produces stronger preference, therefore, the fact that the Reach task had 1,050 trials while the Hasp had only 300 must be considered.

Brookshire and Warren (1962) conclude:

> "...handedness in the rhesus monkey is not a unitary behavioral trait, and is probably the result of a complex of genetic, maturational and other environmental factors [p.227]."

The influence of environmental factors on forepaw preference has been investigated by Cronholm, Grodsky and Behar (1963). They set out to investigate the dependence of lateral preference on certain extra-organismic conditions. They designed a series of tests incorporating in some of them severe restrictions on body movement. The six tests used were:

1. Reach - like Brookshire and Warren's (1962).

2. String - the S had to pull in a string that had the incentive tied to the end (like the String test of Harlow, et. al. (quoted in Kounin, 1938)).

3. Wire - horizontal wire parallel to the front of the cage. Incentive had to be slid off the wire in the direction the wire was pointing.

4. Forced Reach - severe restriction was placed on body orientation. There was an opening to reach out of on the extreme left of the cage and the S was forced into the left of the cage. Similar conditions held for testing the right.

5. Hasp - similar to that of Brookshire and Warren (1962).

6. Handle box - similar to that of Brookshire and Warren (1962).

The results demonstrate that on the Reach task there was a bimodal distribution of preferences with the side of placement of the incentive having little effect on the degree of preference. The String test did not evoke significant preferences. Greater preferences were found on the last four

tasks but this was usually a result of the constraints imposed by the experimental set up. However, a high preference which was disassociated from experimental constraints was shown for the forepaw which pulled the handle in the Handle box test.

Trevarthen (1969) has suggested that for bimanual tasks one hemisphere monitors the action of both hands. For the tasks he describes one hand is used in a supporting role, the other in a manipulative role. He suggests that the controlling hemisphere is contralateral to the manipulative hand. This may be a basis for preferential use of a forepaw in a task involving simultaneous bimanual responses.

It is obvious that the results of the experiments discussed in this section are often conflicting. Simple manipulative tasks have been investigated and shown to produce a greater degree of preference than a simple Reach task (Warren, 1958), but the opposite has also been demonstrated (Brookshire and Warren, 1962). Potentially bimanual tasks, supposedly more difficult than unimanual tasks like the Reach test, have been investigated, but these have been shown to produce a lesser degree of preference than the simple Reach task (Brookshire and Warren, 1962).

Type of forepaw preference:

Early writers on the subject of types of forepaw preference felt that monkeys were either right handed or ambidextrous, with only a few left handed. Ogle (1871) stated that he observed 20 monkeys out of 23 to be right handed with the other three demonstrating left handedness. Langkavel (1874), Martin (1820) and Osawa (1901) had similar opinions expressing the view that the majority of monkeys were either right handed or ambidextrous. On the other hand, Brinton (1896), Cunningham (1902) and Hollis (1874) state that monkeys do not show any decided preference.

Investigating the problem of forepaw preference in rats, Yashioka (1930a, 1930b) obtained a bimodal distribution of forepaw preference with few rats showing ambidexterity. Using 100 rats he had his Ss reach through a hole in a wire mesh and obtain powdered food from a food dish. The hole restricted the S to using one paw. He recorded the number of times each paw went in and out of a hole during two, two minute periods.

Tsai and Mauer (1930) also investigated the problem of forepaw preference in rats but they used a different test. They had the rats reach into a glass bottle to obtain a reward. Only one paw could be inserted into the bottle at one time. From their results they concluded that rats were predominantly right handed.

Working with chimpanzees, Finch (1941) concluded that the incidence of right and left handedness was approximately equal among his Ss with a minority of the Ss displaying ambidexterity. Using the same population of chimpanzees, Yerkes (1943) obtained similar evidence.

Examining the problem of forepaw preference using cats as Ss, Cole (1955) concluded that anatomical structure probably was of more importance in determining forelimb preference than environmental or psychological factors. He had his Ss do two tasks; in one task the Ss had to displace a block to obtain an incentive, in the other task the Ss had to reach into a glass tube to obtain the incentive. More than half of the Ss displayed preferences for the use of one forepaw on more than 75% of the trials (35 Ss out of 60). Of these 12 displayed right preference and 23 displayed left preference. Twenty-five of these Ss were ambidextrous.

From their work with rhesus monkeys, Brookshire and Warren (1962) state their result

> "...reveals an apparently continuous distribution of individual hand preferences....Four monkeys were judged to have a predominantly right hand preference, nine were judged left handed and six were considered either ambidextrous or without definite preference [p.223]."

Ettlinger and Moffett (1964) have suggested that there appears to be a trend towards a greater incidence of left than right lateral preferences in rhesus monkeys, although in their study the difference was not statistically significant.

The more recent studies show there is general agreement that a majority of animals display lateral preferences on specific tasks. The type of lateral preference has not been demonstrated conclusively although there have been some suggestions. It has been suggested that rats display right preferences (Tsai and Mauer, 1930; Yashioka, 1930a, 1930b) and rhesus monkeys display predominantly left preferences (Brookshire and Warren, 1962; Ettlinger and Moffett, 1964).

The object of the present series of experiments is to examine the effect task complexity has on forepaw preferences in monkeys. The main hypothesis under consideration is that complex tasks evoke stronger preferences than do simple tasks. A secondary hypothesis investigated in this series of experiments was that there is a consistent assymetry of forepaw preference for the majority of monkeys.

Investigation of these hypotheses was undertaken in three experiments, the latter ones developed from the former. Experiment I involved a series of three manipulative tasks, Experiment II involved two manipulative tasks and Experiment III involved 12 manipulative tasks.

Experiment I

Introduction:

The three tasks of Experiment I were designed to vary in difficulty of solution in a relatively continuous manner. Test 1 was designed to be the simplest task; it involved obtaining an incentive from an open trough. The task considered to be next in complexity was Test 2; the S had to obtain an incentive from inside a horizontal fixed cylinder. The task considered most complex was Test 3; the S had to obtain an incentive from inside a horizontal, freely hanging, moving cylinder which had to be steadied.

Test 1 was similar to Reach tasks described previously but was adjusted to conform to the testing surface and height used in the other tasks of this experiment. It was designed to control for the restriction of the cylinder for Test 2 and for the restriction and movement of Test 3. Test 2 was designed as a control for the movement involved in Test 3 (that is, the cylinders of both tests were of the same diameter and positioned at the same height). Test 3 was chosen in an attempt to maximize bimanual manipulation.

METHOD

Subjects:

The subjects were ten stumptail macaques (Macaca arctoidea, formerly classified speciosa) which were caught wild. They were at least two and one half years old at the time of testing. Previous training had consisted of adaptation to a restraining chair, training on a simple reaction time task and some adaptation to laterality testing while in the restraining chair.

Apparatus:

Ss were tested in a modified Wisconsin General Test Apparatus (W G T A). The test cage had inside dimensions of 30 x 22.5 x 18 inches. The front and top of the cage had bars two inches apart. The S entered the cage on the experimenter's left. See Figure 1.

The cage was placed on a table. Attached to the table top was a guide for a sliding tray. This guide consisted of two 0.375 inch steel rods parallel to each other 12 inches apart. They were 0.5 inches off the table top and were pointed toward the testing cage.

An aluminum sliding tray 18 x 8 x 0.125 inches was attached to the guide by means of Teflon R blocks that the steel bars slid through. This produced a minimum of noise.

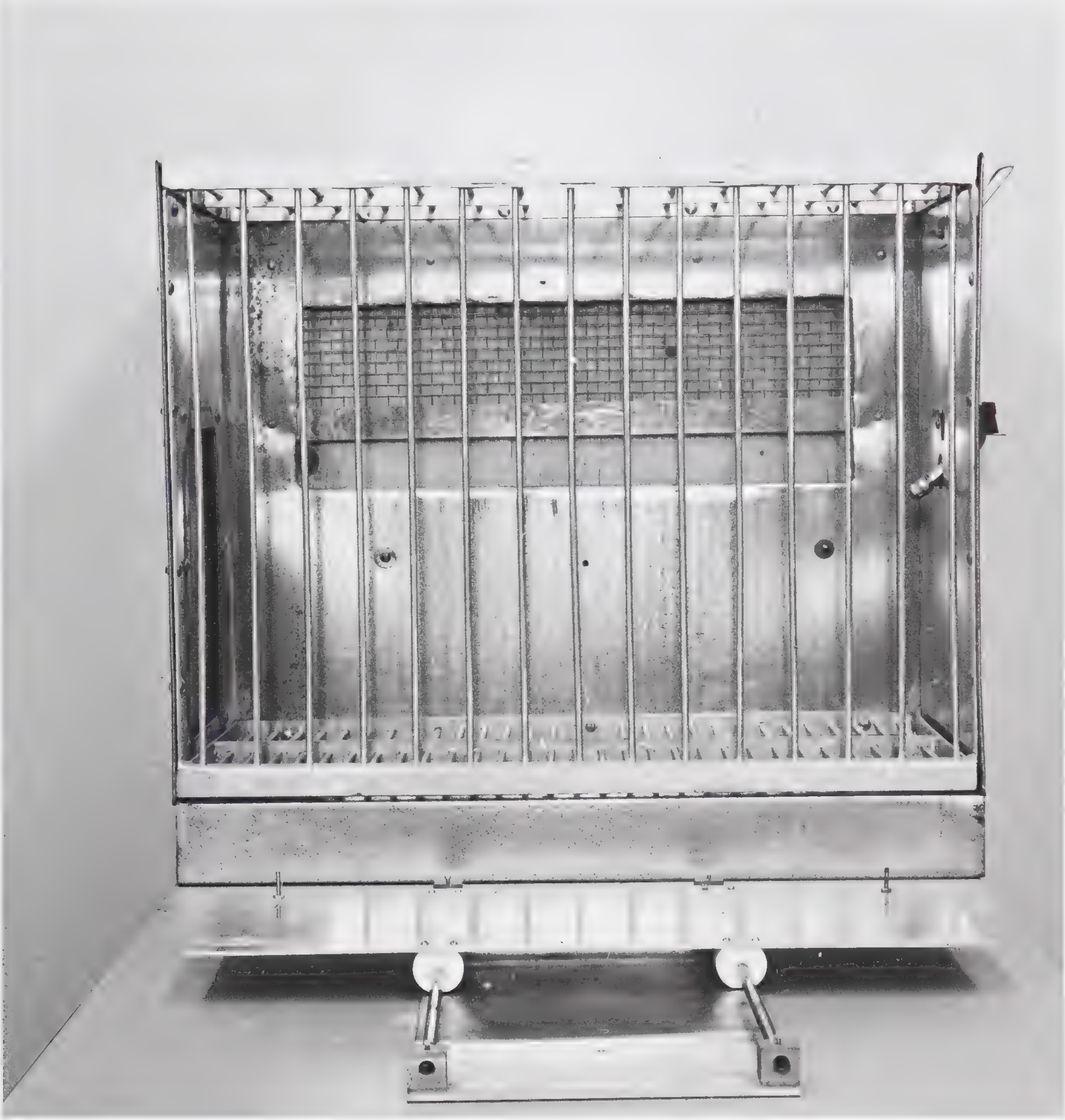

Figure 1: Wisconsin General Test Apparatus.

The sliding tray was designed to accept the attachment of stimulus presentation trays (SPT) which held the manipulanda for each test given to the Ss. The SPT was a piece of 0.5 inch plywood, 10 x 24 inches, to which the manipulanda were attached. The SPT was placed on the sliding tray so that the 24 inch side was parallel to the front of the cage. When the SPT was pushed forward to the full extent, the tray rested against the front of the testing cage.

A description of the manipulanda used for testing forepaw preference follows:

Test 1: Trough - a five inch plexiglas tube, 2.5 inches in outside diameter, two inches inside diameter, was cut in half lengthwise. Each half was attached to the top of separate wooden pedestals. The pedestals were 12 inches high by five inches long by 3.125 inches wide. They were attached to the SPT 12 inches apart measured from center to center and six inches from the edge of the tray to the center of each pedestal. They were 2.5 inches from the front of the tray. The end of each trough away from the front of the SPT was closed with a piece of plexiglas. The S had to obtain the incentive from the trough in which it was placed. This task is similar to the one described by Warren (1953). See Figure 2.

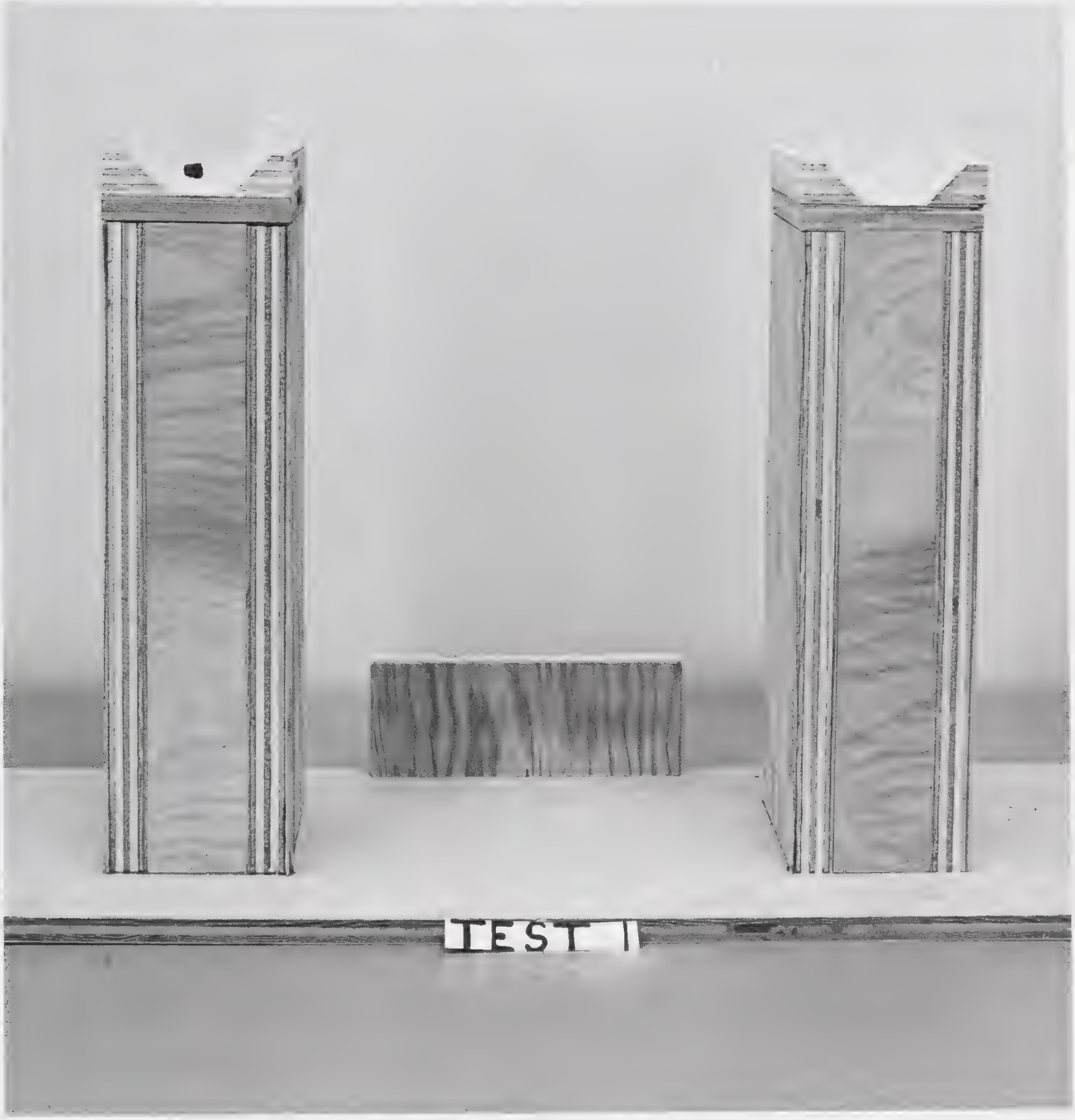

Figure 2: TEST 1 - Trough

Test 2: Fixed cylinder - two plexiglas cylinders of the same dimensions as the one described above were attached to two separate pedestals of the same dimensions as the pedestals described above. The pedestals were attached to the SPT in the manner described above. The end of each cylinder away from the front of the SPT was closed. The S had to obtain the incentive from inside the cylinder. This task is similar to one described by Warren, Abplanalp, and Warren (1967). See Figure 3.

Test 3: Hanging cylinder - two plexiglas cylinders of the same dimensions as those described above were attached by a flexible chain to a bar on a SPT. The bottom of each cylinder was set 12 inches above the SPT. The cylinders were 2.5 inches from the front of the tray and the center of each cylinder was six inches from the side of the tray. The cylinders were 12 inches apart measured from center to center. The end of the cylinder toward the front of the SPT was closed with a circular piece of plexiglas. This meant that the S had to turn the cylinder around in order to obtain the incentive. The S had to obtain the incentive from inside the cylinder. This task was adapted from one described by Jolly (1964). See Figure 4.

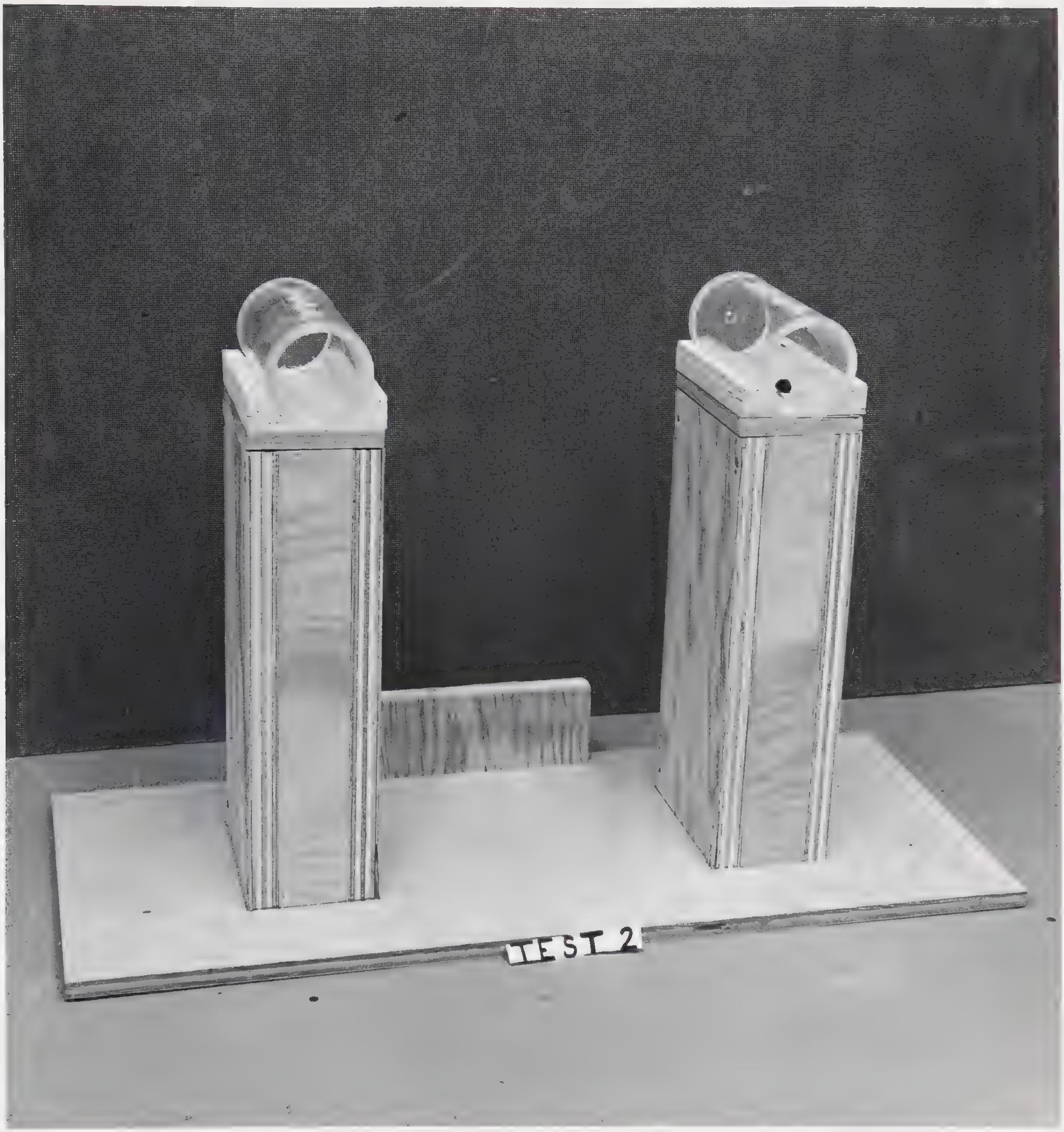

Figure 3: TEST 2 - Fixed Cylinder

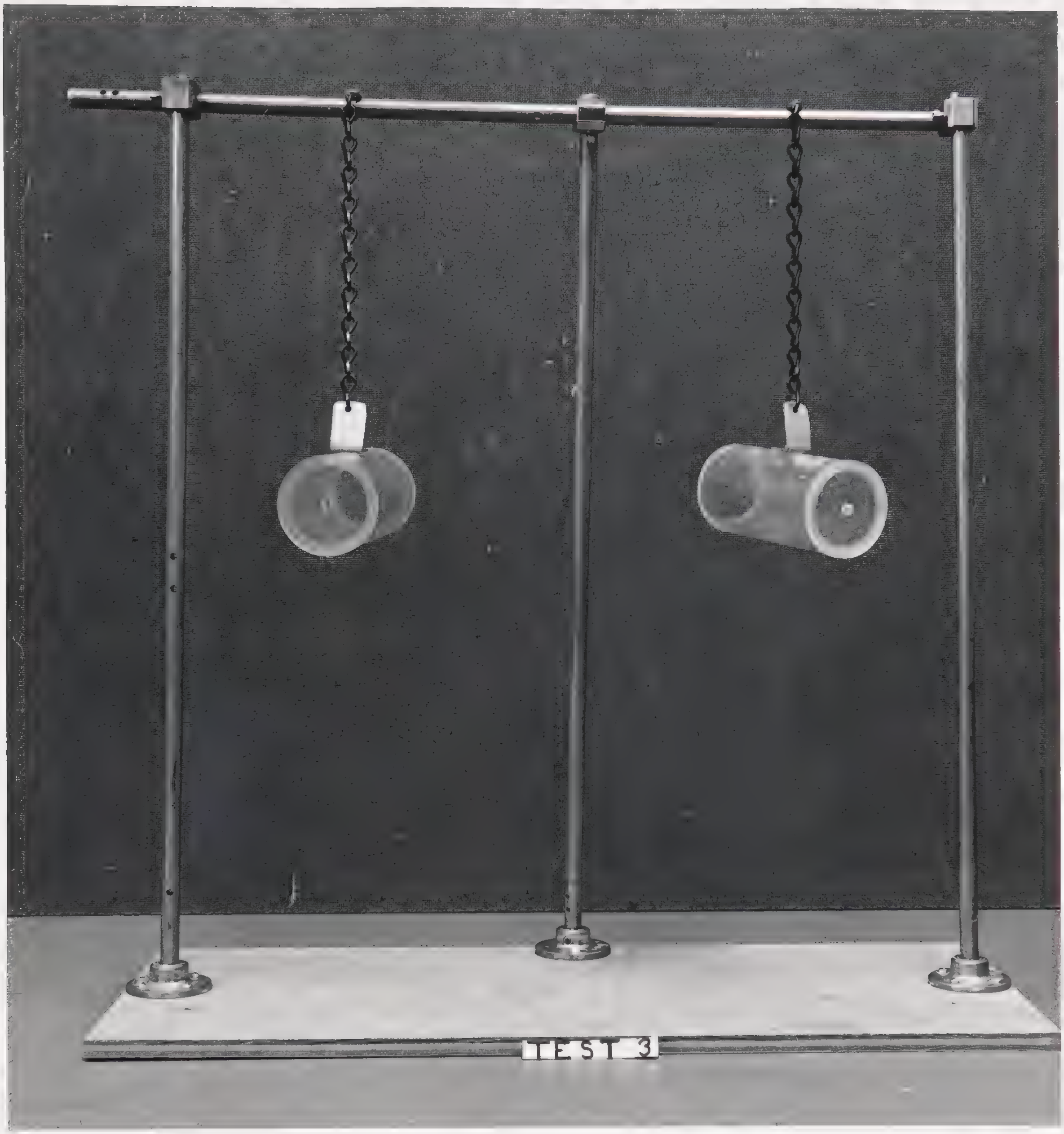

Figure 4: TEST 3 - Hanging Cylinder

Procedure:

Ss were tested after regular testing on simple reaction time. A S was carried into the testing room and placed in the WGTA.

If necessary some shaping trials in the initial session of each test were given but these were eliminated from the results. The criterion for the beginning of recording the responses was five successive correct trials.

The response recorded was the forepaw used to obtain the reward on each trial. Trials on which the incentive was not obtained directly from the cylinder were eliminated and extra trials were given to the Ss to replace these discarded trials.

For the first series, each test was presented on four separate sessions. There were thirty trials in each session with a total of 120 trials for each test. The order of presentation of the tests was random with the constraint that on any session no more than four monkeys could be presented with the same task. The order of placing the incentive on the left or the right side was random in each session.

Test 1 and Test 3 were run as a replication 27 weeks after the tests were first presented. Two 60 trial sessions of each test were presented to each S.

Testing took place in a room next to the colony room. Visual communication with the colony room was eliminated during testing but vocal communication was still present. The *S*s could see the experimenter.

RESULTS

Degree of preference as a function of the test:

The data were scored as a measure of left preference, therefore a high right preference would be scored as a low left preference. Transformations of the data to a percentage deviation score reduced the variance produced by the scoring. The transformation to a deviation score as a percentage was obtained as a deviation from chance performance. For, example, a score of 10% left (L) or 90% L would have a deviation score of 90%. Table 1 presents the deviation scores.

Significant forepaw preference on a test is defined as a deviation in the use of one forepaw by $\pm 3\delta\%$ from chance performance, where $\delta\% = \sqrt{Npq} \times 100/N$ and N=the number of trials, $p=q=\frac{1}{2}$, the probability of right and left responses, assuming no preference. The data, transformed to a percentage deviation, was examined using this criterion. Scores reaching criterion are significant beyond the 0.01 level.

From Table 1 it is apparent that on Test 3 and Retest 3 all Ss demonstrated significant forepaw deviations. Only three Ss showed significant deviations on Test 1 and only two Ss on Retest 1. On Test 2 only two subjects showed significant deviations.

DEVIATION SCORES

Monkey	Test 1	Retest 1	Test 2	Test 3	Retest 3
1	56.7	62.5	62.5	100*	100*
2	52.5	87.5*	54.2	73.3*	82.5*
3	55.0	58.3	53.3	71.7*	82.5*
4	70.8*	64.2*	52.5	70.0*	74.2*
5	57.5	84.2*	53.3	83.3*	92.5*
6	70.8*	63.3	52.5	100*	100*
7	54.2	60.8	71.7*	96.7*	85.0*
8	53.3	53.3	62.5	100*	100*
9	50.8	52.5	69.2*	99.2*	100*
10	88.3*	63.3	87.5*	80.8*	82.5*

* $p < 0.01$

Table 1: Deviation score in percentage by individual monkeys.

Figure 5 is a plot of the median deviation score and inter-quarterile range (IQR) on each test. The combination of a high median on a short IQR indicates a test producing strong deviations.

Using the Wilcoxon matched pairs signed-ranks test (Siegel, 1967) to analyze differences in degree of deviation produced by the tests, Test 3 was found to differ significantly from both Test 1 and Test 2 ($T=3$, $n=10$, $p<.01$). Test 1 and Test 2 do not differ significantly.

Table 2 presents the Spearman correlations between the tests of the initial series. There were no significant correlations.

Table 3 presents the Spearman rank-order correlations for test-retest reliability for Test 1 and Test 3. (Test 2 was not presented in the retest series.) This demonstrates that Test 1 does not reliably produce a specific degree of preference while Test 3 does. The means of the test-retest deviation scores illustrate that Test 3, the Hanging Cylinder, produces the larger deviations (Table 1, Figure 5).

<u>Laterality preference as a Function of the Test</u>. The data was transformed to a percentage use of the left forepaw and the results are presented in Table 4 as Laterality scores. The total number of trials on each test is 120.

From Table 4 it is apparent that left preferences predominate. Overall there were seventeen significant left preferences compared to twelve significant right preferences. Fourteen of the left preferences and six of the right preferences were displayed on Test 3 and Retest 3, eight left and two right on Test 3, six left

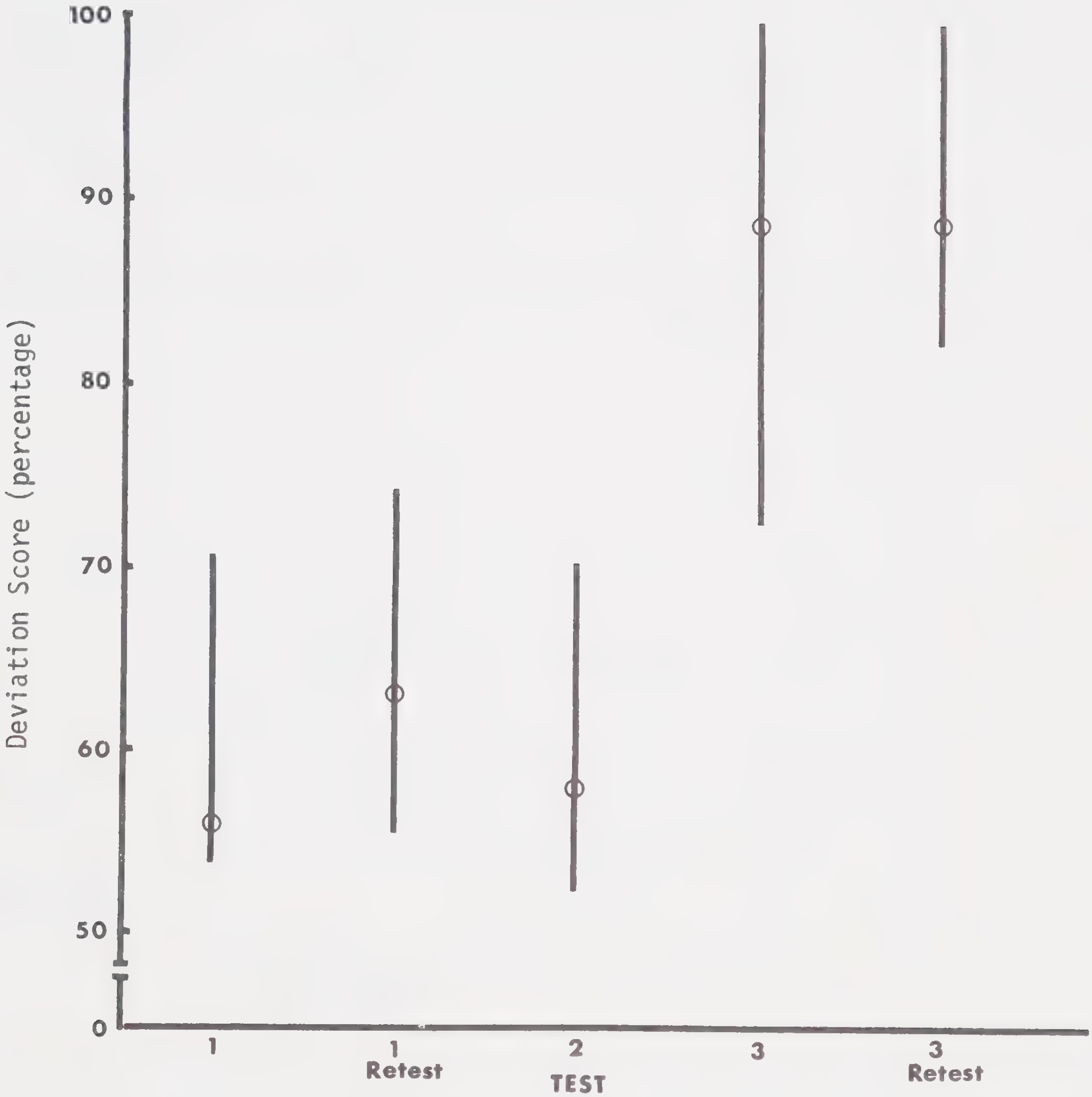

Figure 5: Deviation Produced on the Tests. (In this Figure and in Figures 8 and 21, each circle represents the median deviation score on one test and the bar represents the Interquartile Range on that test).

	TEST 2	TEST 3
TEST 1	0.42	0.24
TEST 2		0.26

Table 2: Correlation of deviation scores between tests.

	RETEST 1	RETEST 3
TEST 1	0.026	
TEST 3		0.872*

* $p < 0.005$

Table 3: Retest reliability on deviation scores

LATERALITY SCORES

Monkey	Test 1	Retest 1	Test 2	Test 3	Retest 3	Significant Preference R	Significant Preference L
1	56.7	62.5	62.5	100*	100*	0	2
2	52.5	12.5*	54.2	73.3*	17.5*	2	1
3	45.0	41.7	53.3	28.3*	17.5*	2	0
4	70.8*	35.8*	47.5	70.0*	25.8*	2	2
5	42.5	15.8*	53.3	83.3*	92.5*	1	2
6	29.2*	36.7	47.5	100*	100*	1	2
7	45.8	60.8	28.3*	3.3*	15.0*	3	0
8	53.3	46.7	37.5	100*	100*	0	2
9	49.2	52.5	30.8*	99.2*	100*	1	2
10	88.3*	36.7	87.5*	80.8*	82.5*	0	4
Significant Preference							
R	1	3	2	2	4	12	
L	2	0	1	8	6		17

* $p < 0.01$

Table 4: Percentage left forepaw use by individual monkeys.

and four right on Retest 3. There were two reversals of laterality preference on Test 3: two monkeys changed from significant left preferences of the first presentation of Test 3 to significant right preferences on the retest of Test 3. On Test 1 one S reversed preference and another nearly did.

Discussion

The Degree of Deviation as a Function of the Test. The present experiment showed that Test 3, the Hanging Cylinder, produced the greatest degree of forepaw preference (Table 1, Figure 5). This test involves the simultaneous use of both forepaws and a moveable manipulanda which were judged to make it more complex than Test 1, the Fixed Trough or Test 2, the Fixed Cylinder: both involve fairly simple unimanual responses. Test 3 differs significantly from both Test 1 and Test 2 while they do not differ significantly from each other in the degree of preference produced. Also Test 3 reliably produces a high deviation score while Test 1 does not (Table 3). These results support the hypothesis that the more complex task, Test 3, would produce the strongest preferences. They are also in agreement with the conclusion made by Kounin (1938) "... that those [tests] which manifest the greatest degree of hand preference demand more difficult, refined or complex manipulations [p. 392]", and with the results of a study done by Warren (1958) in which he found that complex tasks elicited a higher proportion of monkeys displaying significant preferences.

Although the results of Experiment I disagree with the findings of Brookshire and Warren (1962) there is a possibility that a practice effect may have confounded the preference results on their Reach test. This would make that test appear to elicit stronger preferences than their potentially bimanual tasks; Warren (1958) demonstrated that practice effects produce stronger preferences. They gave 1,050 trials on the Reach task but only 300 trials on two of the

potentially bimanual tasks and 150 trials on the other. Their conclusion that complex tasks do not produce stronger performance is somewhat suspect due to this confounding effect.

The high retest reliability (Table 3) and the high median (Figure 5) of Test 3 demonstrate that it is consistant in producing high deviation scores. This also supports the hypothesis that tasks involving complex manipulations produce stronger forepaw preferences.

Laterality preference as a function of the Test. The results of Experiment I suggest that a preference for the use of the left forepaw is predominant in the monkeys tested. There were seventeen significant left preferences compared to twelve significant right preferences (Table 4). This agrees with reports in the literature of a predominant preference for left forepaw use among monkeys (Ettlinger 1961, Ettlinger and Moffett 1964, Milner, 1969). The large majority of the significant preferences in Experiment I were produced on Test 3, the Hanging Cylinder (Table 1).

No explanation for the predominant use of the left forepaw can be derived from the data obtained in Experiment I. Although Gautrin and Ettlinger (1970) have suggested that left preference is associated with visual control of responses, incidental observations in the present experiment suggest that their hypothesis may not be tenable. On most of the tasks Ss did not seem to closely attend, visually, to the incentive when reaching into the manipulanda to obtain the incentive. In fact, especially on the Fixed Cylinder and the Hanging Cylinder tests, the forepaw usually concealed the incentive from view.

A second experiment was designed to investigate what, if anything, produces predominant preferences which are general throughout the species.

Experiment II

Introduction

Suggestions that left preferences predominate in monkeys (Ettlinger 1961, Ettlinger and Moffett 1964, Gautrin and Ettlinger, 1970, Milner 1969, Warren 1958, Experiment I) raises the question of what is causing the bias toward this side. Are there response patterns associated with task characteristics which result in this bias? Experiment II was designed in an attempt to examine whether task characteristics were associated with production of a predominant bias toward preference for the use of one forepaw.

Napier (1956, 1960) described two types of grip in man: a power grip and a precision grip. He said, "The precision grip is employed where delicacy and precision of movement are required; the application of muscular power being a secondary consideration. In contrast, the dominant characteristic of the power grip is the application of force; delicacy and precision being of secondary importance [p. 648]" (Napier 1960). This distinction may lead to the suggestion that there may be a preference for the use of one forepaw in tasks requiring precision and for the other forepaw for tasks requiring power. In examining the precision-power grip dichotomy in anthropoid apes Napier (1960) confines himself to dealing with considerations of muscular and skeletal anatomy. He states that they have difficulty in opposing the thumb and forefinger but that this is largely due to the shortness of the thumb. This difficulty results in a poor precision grip, usually accomplished by contact between fingers rather than digit-thumb opposition. The power grip of anthropoid apes

is accomplished solely by a flexion of the fingers.

In 1967 Napier describes an opposability index which indicates the ability of digit-thumb opposition of primates. On this index macaca species ranks high, just below baboons which rank just beneath humans. This would suggest that Napier's (1960) description of precision-power grips in man may be more applicable to macacas than to anthropoid apes because the thumb may be involved more in the grips of the former.

A secondary problem, which is considered in the next experiment, is the apparent contradiction between the incidental observations in Experiment I and the hypothesis put forward by Gautrin and Ettlinger (1970). Two tests were developed and administered to the Ss in order to examine the problems described above. One of the tests, the Brush Test, was designed to approximate the naturalistic act of grooming; the other test, the Drawer Pull, was designed to incorporate simultaneous bimanual manipulation and some visual guidance of behavior. The Drawer Pull test was adapted from a test by Cole (1957).

The test approximating grooming was chosen because this is a well-practised response in stump-tailed macaques which appears to require precise manipulations and visual guidance. Grooming is done using both hands with the use of one hand to part the hairs with a brushing motion and the other hand to do the fine manipulations involved in removing the particles found. The precision grip would be involved in the fine manipulations while something like the power grip might be involved in the brushing movements because of the simple flexion

type responses involved i.e. rather than a power as such this response may involve flexion.

The Drawer-Pull task was chosen because of the tonic aspect of holding the drawer open. This part of the response was interpreted as incorporating the power grip suggested by Napier (1960). Obtaining the incentive from the small food well might be interpreted as involving the precision grip.

METHOD

Subjects. The Ss were the same 10 Macaca arctoidea as used in Experiment I. Previous training was as described in Experiment I with the addition of training on the initial series of tests from Experiment I.

Apparatus. Ss were tested in a modified WGTA (EXP. I). The manipulanda for the tests in Experiment II were on SPT which the sliding tray of the WGTA. A description of the manipulanda follows:

Test 4 - The Brush Test. One dusting brush was cut into two 4 1/2 inch segments. The segments were 1 1/2 inches wide and the bristles were 1 1/4 inches long. The pieces of brush were attached to wooden pedestals like those described in Experiment I but the brush was attached to the front of the pedestal with the longitudinal axis parallel to the front of the SPT and the testing cage. (Figure 6).

Test 5 - The Drawer Pull. Two drawer-like manipulanda were made by inserting two plexiglas tubes with two inch outside diameters inside plexiglas tubes with two inch inside diameters. A slot was cut on each side of the outside cylinder and pins were inserted through these slots into the inside cylinder to act as guides to steady the inside cylinder. The inside cylinder was counterweighted to retract if pulled out, then released. (Figure 7).

A food well was set into the top of the inner cylinder, 2 1/2 inches from the front. The well was 3/4 inches in diameter and 1/2 inch deep. When the smaller cylinder was retracted the food well was covered by the large cylinder.

Figure 6: TEST 4 - Brush

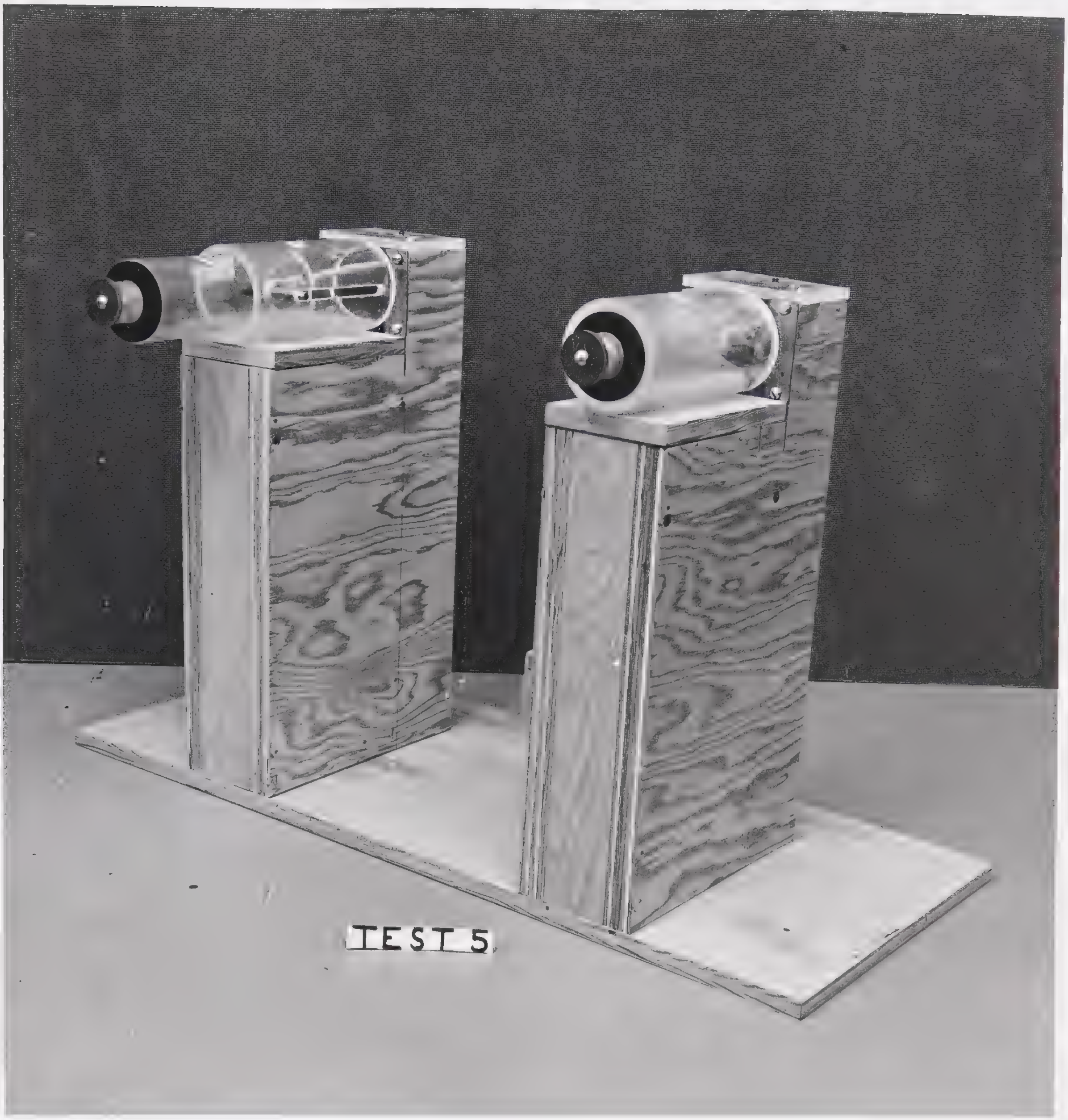

Figure 7: TEST 5 - Drawer Pull

A knob 3/4 of an inch in diameter and 3/4 of an inch long was attached to the front of each smaller cylinder. A 1 1/4 inch circle of 1/8 inch plastic, painted red, was attached to this.

Procedure

The procedure was similar to that in Experiment I but Tests 4 and 5 were used instead of Tests 1, 2 and 3.

For Test 4 the incentive was placed between the bristles at a depth of at least 1/2 inch. The S had to part the bristles to find the incentive.

Performance on the Brush Test, Test 4, was scored by which forepaw first reached out to part the bristles (M) and which forepaw obtained the incentive (I). M refers to responses involving manipulation measures, I to responses involving obtaining the incentive.

In Test 5 the incentive was placed in the well on top of the drawer. The drawer had to be pulled forward so the incentive could be taken from the well.

Performance on Test 5, the Drawer Pull, was scored by which forepaw pulled on the handle (M) and which forepaw obtained the incentive (I).

RESULTS

Degree of Preference as a Function of a Test. As in Experiment I the data was scored as a measure of left preference. The same transformation as used in Experiment I was applied to the data of Experiment II to reduce the variance caused by the scoring technique. The resulting preference scores are tabulated in Table 5.

Using the Wilcoxon matched pairs signed-ranks test no significant differences were found between Test 4 and Test 5 on the number of monkeys exhibiting forepaw preferences when obtaining the incentive or when manipulating the manipulanda.

Figure 8 is a graph of the Interquartile Ranges (IQR) and medians of the responses to Test 4 and Test 5. This demonstrates the overlap in the production of preferences by the two tests and also shows that, except for the measure of manipulation on Test 4, the medians are fairly closely grouped.

Laterality of Preference as a Function of the Test. Table 6 contains the data from Test 4 and 5 as the percentage left responses. Significant forepaw preference was defined, in Experiment I, as $\pm$ 36% This criterion is used again in this Experiment.

Examination of Table 6 demonstrates that all significant preferences on the I responses are left preferences (11 significant left preferences out of a total of 20 possible, no significant right preferences).

Most of the significant preferences on M responses are right preferences (Table 6). There are 13 significant right preferences and 3 significant left preferences from a total of 20 possible. One S

	TESTS			
	4		5	
Monkey	M	I	M	I
1	83.3*	60.0	94.2*	91.2*
2	65.0*	53.3	51.7	54.2
3	78.3*	78.3*	52.5	58.8
4	70.0*	55.8	73.3*	72.5*
5	88.3*	90.9*	73.3*	85.8*
6	63.3	55.8	58.3	60.0
7	73.3*	74.2*	95.0*	94.2*
8	89.2*	68.3*	95.8*	95.8*
9	95.8*	95.8*	96.7*	62.5
10	100*	66.7*	70.8*	61.7

* $p < 0.01$

Table 5: Deviation score (percentage) by individual monkeys

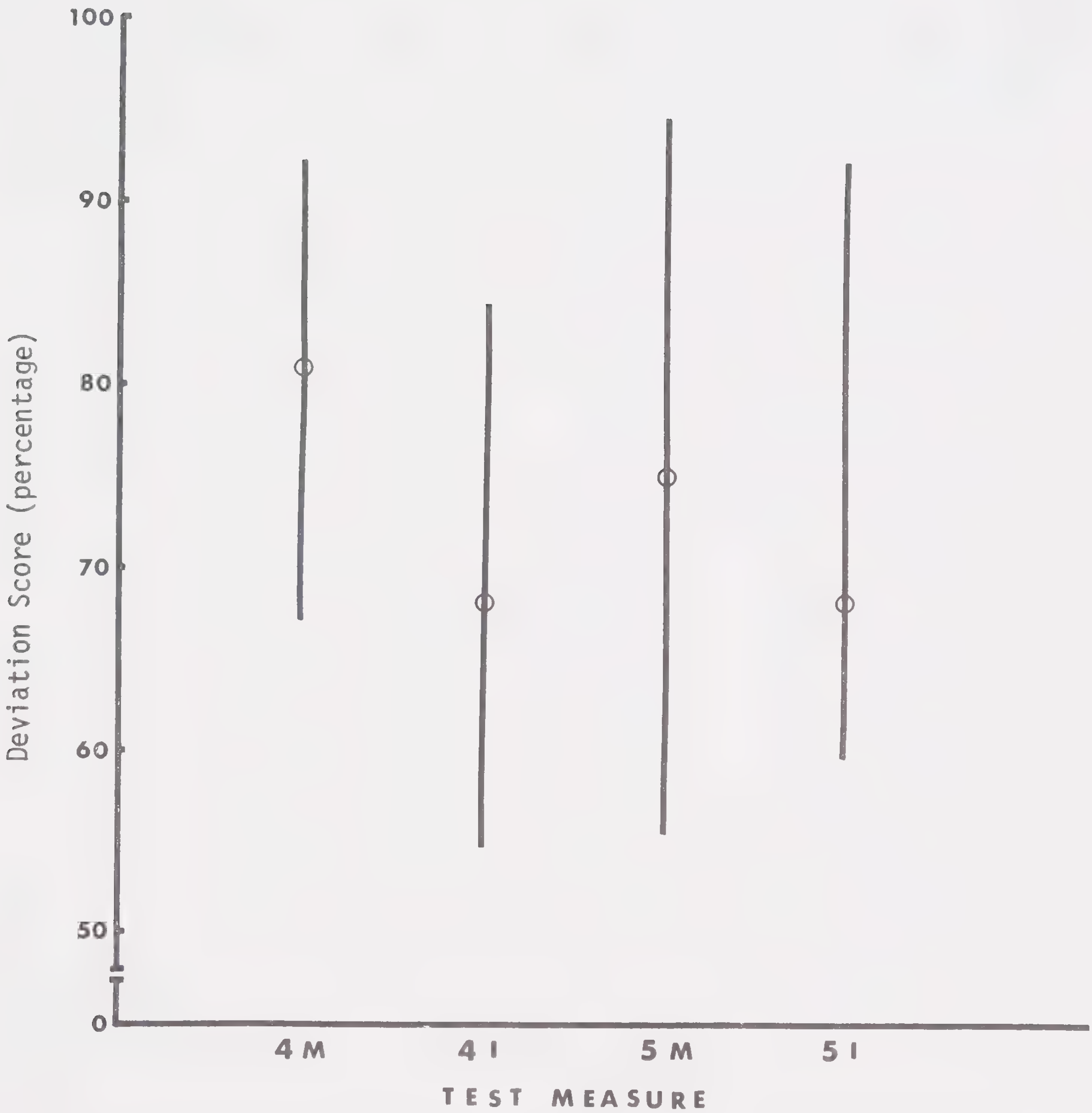

Figure 8: Interquartile Range and Median Deviation Score on the Test Measures.

	TEST 4 M	TEST 4 I	TEST 5 M	TEST 5 I	SIGNIFICANT PREFERENCE R	L
N	120	120	120	120	R	L
±3 %	13.7	13.7	13.7	13.7		
1	16.7*	60.0	5.8*	91.2*	2	1
2	6.5*	53.3	51.7	45.8	0	1
3	21.7*	78.3*	47.5	41.2	1	1
4	30.0*	55.8	26.7*	72.5*	2	1
5	11.7*	90.8*	26.7*	72.5*	2	1
6	36.7	44.2	58.3	40.0	0	0
7	26.7*	74.2*	5.0*	94.2*	2	2
8	10.8*	68.3*	4.2*	95.8*	2	2
9	4.2*	95.8*	76.7*	37.5	1	2
10	100*	66.7*	70.8*	38.3	0	3
Significant Preference						
R	7	0	5	0	12	
L	3	6	2	5		16

* $p < 0.01$

Table 6: Percentage left forepaw responses by individual monkeys.

made two of the significant left preferences (S 10).

Table 7 presents the Spearman rank order correlations on the laterality data between all measures on the tests. The only significant correlations is the highly significant negative correlation between the different measures of Test 5. This indicates that opposite forepaws are used for the separate measures on this test.

TEST	4 I	5 M	5 I
4 M	-0.443	0.448	-0.470
4 I		0.092	0.071
5 M			-0.958*

* $p < 0.005$ df=8, T= 9.45

Table 7: Correlation of test measures.

DISCUSSION

Degree of Deviation as a Function of the Test. Experiment II showed no significant differences in degree of deviation between the two tests for either measure of forepaw preference: obtaining the incentive or manipulation of the manipulanda. Examination of the means and IQR demonstrated that although there was overlap in the production of deviations, there was a tendency for Test 4 to produce stronger deviations on the measure of manipulation. (Table 5 Figure 8).

Comparing the measurement of which forepaw obtained the incentive on Tests 4 and 5 (Table 5) to the same measurements on Tests 1, 2 and 3 in Experiment I (Table 1), it can be seen that Tests 4 and 5 produce stronger preferences than Tests 1 and 2 but weaker preferences than Test 3, but the differences are not significant by the Wilcoxon signed-ranks test (Siegel, 1967).

The nonsignificant difference between Tests 4 and 5 was not unexpected because both were designed to be complex in an attempt to produce greater degrees of deviation. Since they were designed to involve some manipulative skill, thus being more difficult than Tests 1 and 2, it was to be expected that they would produce stronger deviations than Tests 1 and 2.

An explanation of why Tests 4 and 5 did not produce deviations as strong as those produced by Test 3 may be that the bimanual manipulations involved in Tests 4 and 5 were not as complex as the bimanual manipulations of Test 3. For example, the manipulanda of Test 5 moved only back and forth while for Test 3 it moved in many

planes. A difference in the complexity of the manipulation between Test 4 and Test 5 may be the explanation of the tendency for Test 4 to produce stronger deviations on this measure than does Test 5.

In Test 4 the parting of the bristles is an active M response while in Test 5 holding the drawer open is a static M response. Test 3, like Test 4, invoked an active response. If active M responses are more complex than static M responses then the tendency for Test 4 to produce stronger deviations than Test 5, and the stronger deviations on Test 3, than on Test 4 or Test 5 could be explained. The simultaneous use of both hands, one in a supportive or steadying role, in Test 3 may involve more complex interactions than the interactions involved in the potentially bimanual responses in Test 4 of parting the bristles and obtaining the incentive.

It was suggested that M responses contained characteristics of Napier's (1960) power grip while I responses would involve his precision grip and that these grip types may be preferentially associated with one or the other forepaw. The results of the present tests involving M and I responses suggest that these characteristics may be relevant for producing deviations. It was decided that further examination of preferences using tasks which incorporate the precision power dichotomy was necessary.

<u>Laterality of Preferences as a Function of the Test</u>. The results of Experiment II suggest that the characteristics of the I and M responses on Tests 4 and 5 separate forepaw use into predominately left or right, dependent on the task characteristics. The M responses were predominately right (13 significant right, 3 significant left,

out of a possible 20 responses), while the I responses were predominately left (11 significant left responses, 0 significant right responses out of a possible 20 responses).

If the I and M responses are examples of the precision power dichotomy this may be interpreted as one hemisphere controlling the precision grip while the other hemisphere is involved in controlling the power grip. If this interpretation is accepted there may be no 'dominant' hemisphere as such; each hemisphere may control responses which have different functional characteristics. The correlations between the measures of each task lend some support to this interpretation. There is a negative correlation between the M and I measures in each test, but only in Test 5 is this correlation significant. ($r=-.958$, $p<.005$, Table 7). Although the number of Ss with common significant preferences on the M measure of both tests or the I measure of both tests suggest that different hemispheres are associated with the two measures, the correlations do not support this. There should be a high correlation between the two M measures and the two I measures; there is a medium correlation between the M measures ($r=.448$, Table 7) and a very low correlation between the I measures ($r=.071$, Table 7).

A third exploratory experiment was done to examine further the possibility of differences between the M and the I measures that would indicate the association of one forepaw or the other predominately with one measure.

Experiment III

Introduction

The final experiment in this series was designed both to explore the relationship between task characteristics and the production of forepaw preferences, specifically to examine which characteristics are associated with left responses and which with right responses, and to further examine the effect of task complexity on the production of deviations.

Most of the tests were designed with the intent of incorporating measures of both fine manipulation and coarser manipulations. The basic structural component of most of the tests was a plexiglas box with a latch on the front. The S had to open the latch in order to obtain an incentive from the box. Measures involved recording which forepaw manipulated the latch to open it (M) and which forepaw obtained the incentive (I).

Complexity for this experiment was determined by a subjective judgement of the Experimenter. It has been vaguely defined by other investigators; Cole (1957) described a "skilled" response as involving opening a drawer and Warren (1958) described removing a block from over a food well and obtaining food from the well as more complex than obtaining the food from the well. In the present experiment complexity was defined as the degree of involvement of two manipulative features in a task; simultaneous use of both forepaws necessitated by a moveable manipulanda and chaining of responses. The series of tests presented were deceloped to investigate the effects these features have on laterality preference. One hypothesis entertained was that more complex

tasks (i.e. those involving chained responding and simultaneous use of both forepaws) should produce greater deviations from chance than the more simple tasks. Asecond hypothesis concerned laterality preference. It was hypothesized that there would be a bias to one forepaw on the manipulation (M) measures and a bias toward the other forepaw on the incentive (I) measures.

METHOD

Subjects

The Ss were the same 10 *Macaca arctoidea* as the ones in the previous two experiments.

Apparatus

Ss were tested in a modified WGTA (Experiment I). The manipulanda were on SPT's which fitted the sliding tray of the WGTA. The manipulanda were as described below:

Test 6 - Fixed Latch Box. Two boxes made of transparent plexiglas were attached to the SPT. Each box was a 4.5 inch cube with a hinged lid. A hasp was attached to the lid at the front of the box. The hasp had a tongue (2.5 inches long and 1 inch wide) which fitted over a staple and was held there by friction only. The lower .75 inches of the tongue was painted red. All plexiglas boxes in subsequent tests were of the same dimension. (See Figure 9).

The lid was spring loaded so that when the hasp was pulled off the catch the lid opened. The lid could not open more than .45 degrees because it was stopped by an aluminum guard. (See Figure 10).

The hinge part of the tongue of the hasp had enough friction for the tongue to stay where positioned. This usually kept the hasp out of the way of the S. The boxes were set 11.875 inches apart center to center, 1.75 inches from the front of the SPT. The reward was placed in the box through a hole in the lid. (See Figure 11).

Test 7 - Hanging Latch Box. Two boxes of the same dimensions and construction as those in Test 6 were used. Instead of being fixed to the SPT they were hung via a pulley system so that the S had to pull

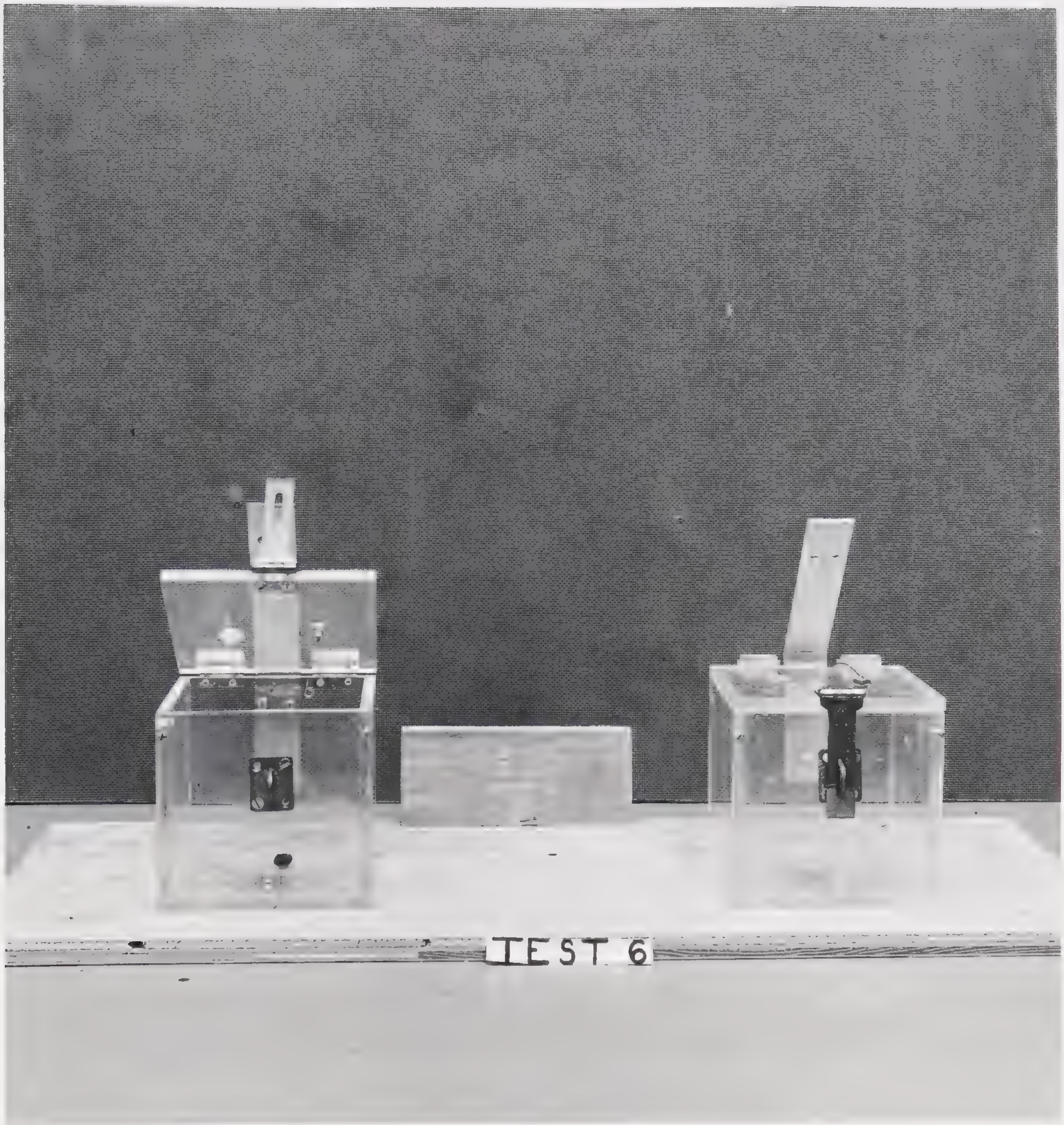

Figure 9: TEST 6 - Fixed Latch Box

Figure 10: Detail of Latch

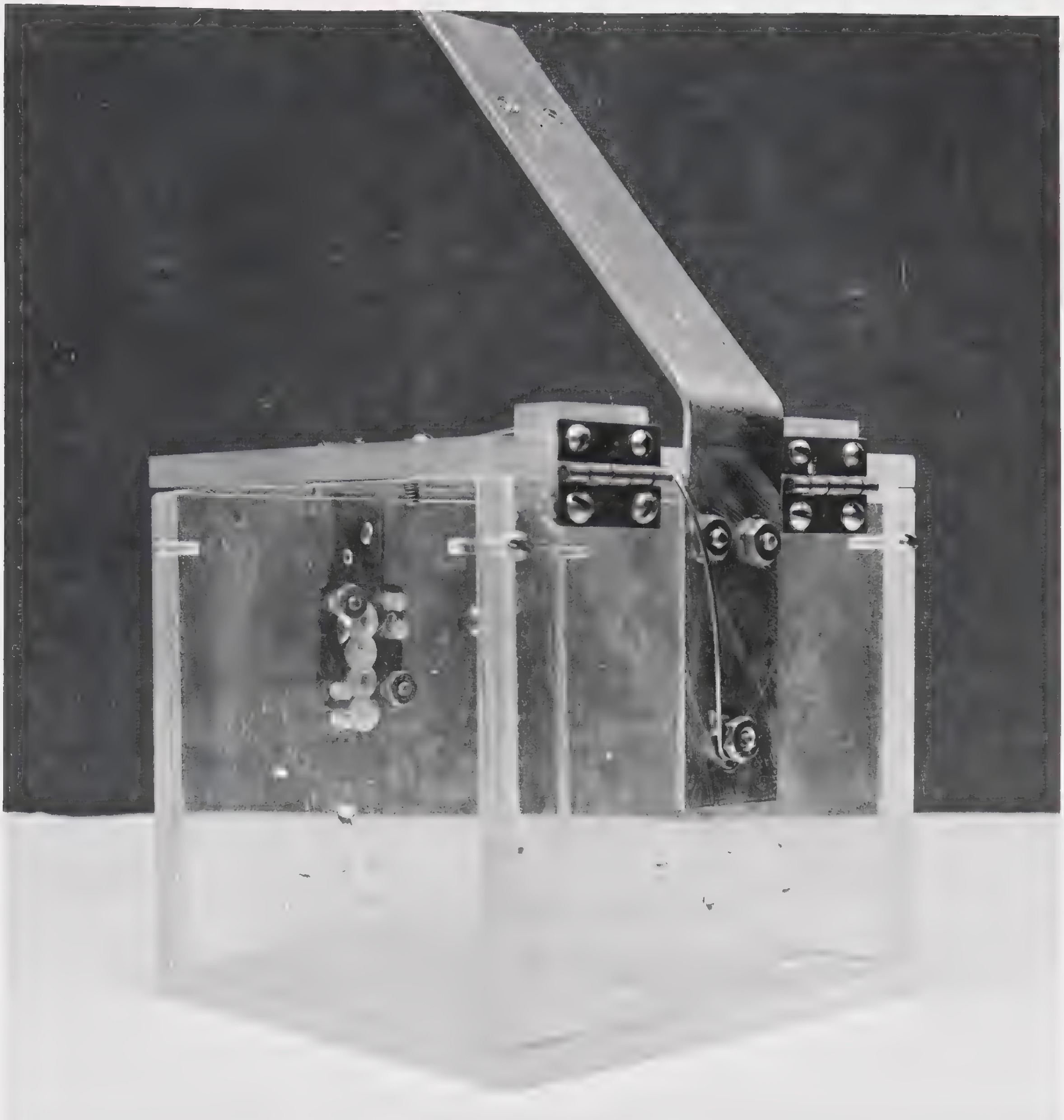

Figure 11: Detail of Lid Spring

the box down to open it. The boxes were counterweighted to return to the starting position if released. (See Figure 12).

The overall height of the manipulanda with the SPT was 36.25 inches. The maximum height of a box from the top of the SPT to the top of the box lid was 30.5 inches. The minimum height of the box from the top of the SPT to the top of the box lid was 4.5 inches (ie. the box rested on the SPT).

A guide was attached to the back of the box to keep the box generally oriented toward the S. The guide was a block of wood 2 inches X 1.5 inches X .75 inches with a .875 inch hole drilled in it .375 inches from the back of the box and .562 inches from the edges of the block. The hole was lined with a plastic tube to reduce friction. A .5 inch steel bar was inserted through the hole as a guide pole. Guides for the counterweight were mounted in a similar manner. (See Figure 13).

The front of the box was 1.75 inches from the front of the SPT. The centers of the boxes were 11.875 inches apart. The guide poles for the box and counterweights were 5 inches apart center to center. The hasp was attached in the same manner as that in Test 6. The rope from which the box hung was attached to the aluminum guard which stopped the lid from opening more than 45^{o}. The box hung level. The incentive was placed inside the box through a hole in the lid.

Test 8 - Two Latch-Box Shallow Bottom. Two hasps were put on the front of each box, over the same catch. One hasp was hinged at the bottom of the box, the other was hinged at the top as in Test 6. The hasp hinged at the top was put over the catch first, then the hasp

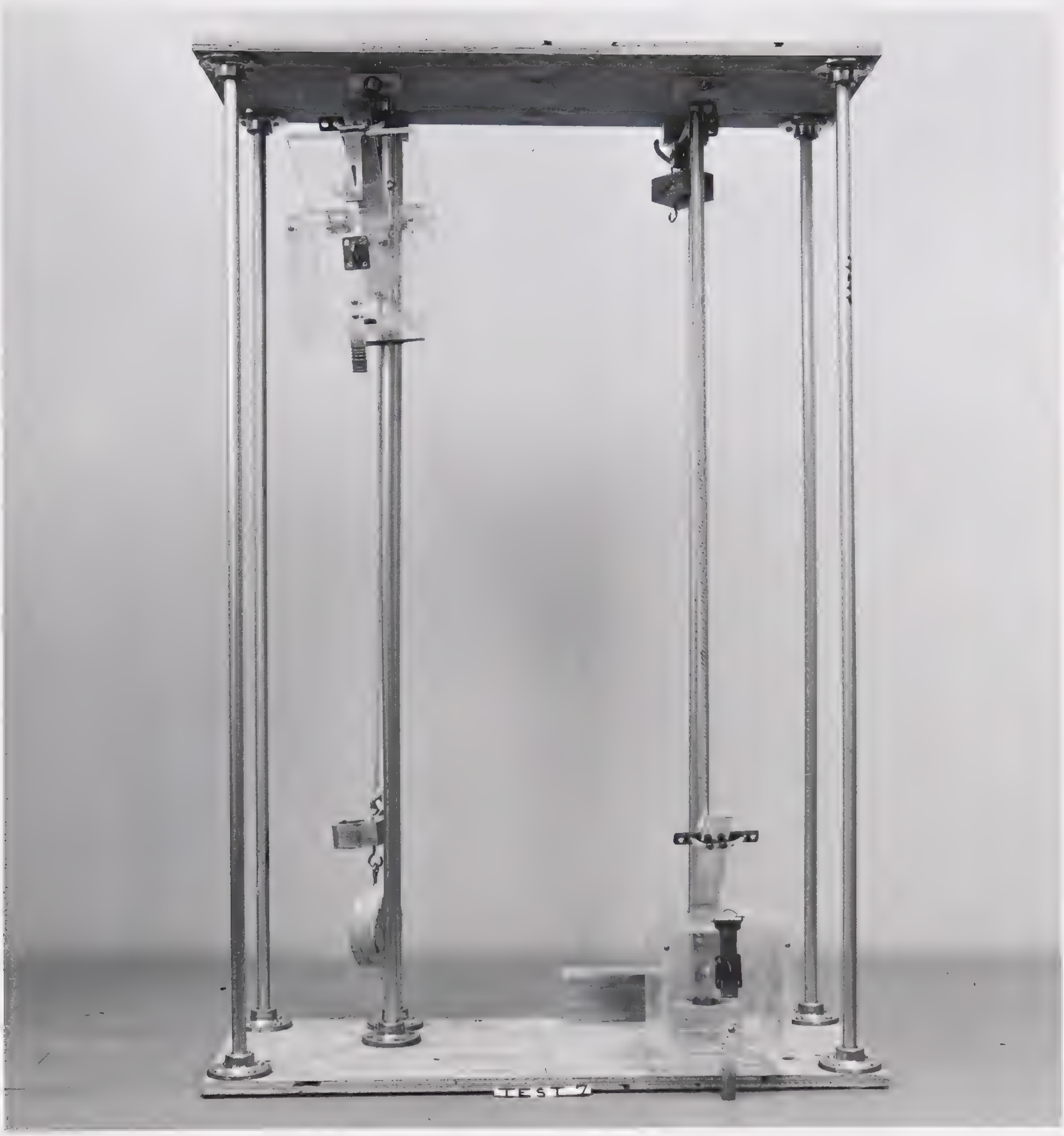

Figure 12: TEST 7 - Hanging Latch Box

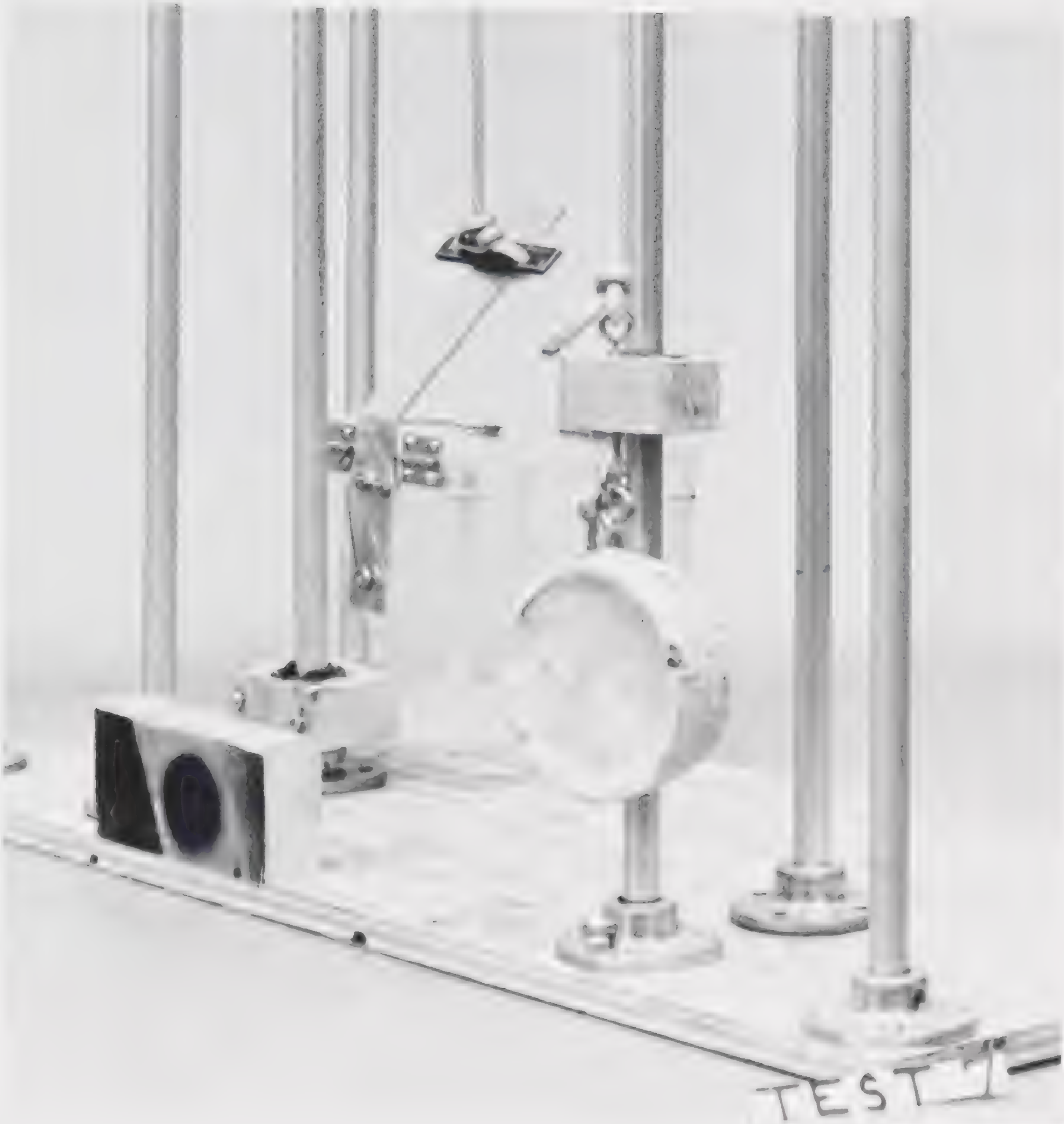

Figure 13: BACK VIEW TEST 7 - Guide Posts

hinged at the bottom was put on top of it (See Figure 14).

A false bottom was put in each box 3.5 inches above the previous floor. This made the depth of the box essentially 1/2 inch on this test (See Figure 14). The incentive was placed on the false bottom when the lid was open.

Test 9 - Opaque Box. Two boxes of the same dimensions as those used previously (eg. Test 6) were covered with masking tape to make them opaque. The lid was left open and the incentive was placed on the floor of the box.

Test 10 - Inlaid Two Latch Box. Two boxes had two hasps attached to them like the hasps in Test 8. In addition, .25 inch plastic guards were placed along side the hasps to necessitate opening the hasps from the front, not the sides (See Figure 15).

Test 11 - Hanging Inlaid Two Latch Box. Two boxes like those in Test 10 were attached to the SPT to hang like the boxes in Test 7.

Test 12 - Rotating Hairy Boxes. Two wooden boxes 2.5 inches wide, 3 inches high and 5.25 inches long were attached on swivels to the SPT. The floor of the box was 12 1/4" above the SPT. One end of the box was open and the box was lined with fur. The box could swivel through 360 degrees (See Figure 16).

Test 13 - Open Transparent Box. Two of the standard transparent boxes were fixed to the SPT and the incentive was placed on the floor. The lid of the box was left open (See Figure 17).

Test 14 - Open Box Shallow Bottom. The boxes were identical to those in Test 8; however, the lid of the box was left open (See Figure 14, Figure 17).

Figure 14: Detail of Shallow Bottom

Figure 15: Detail of Inlaid Latch

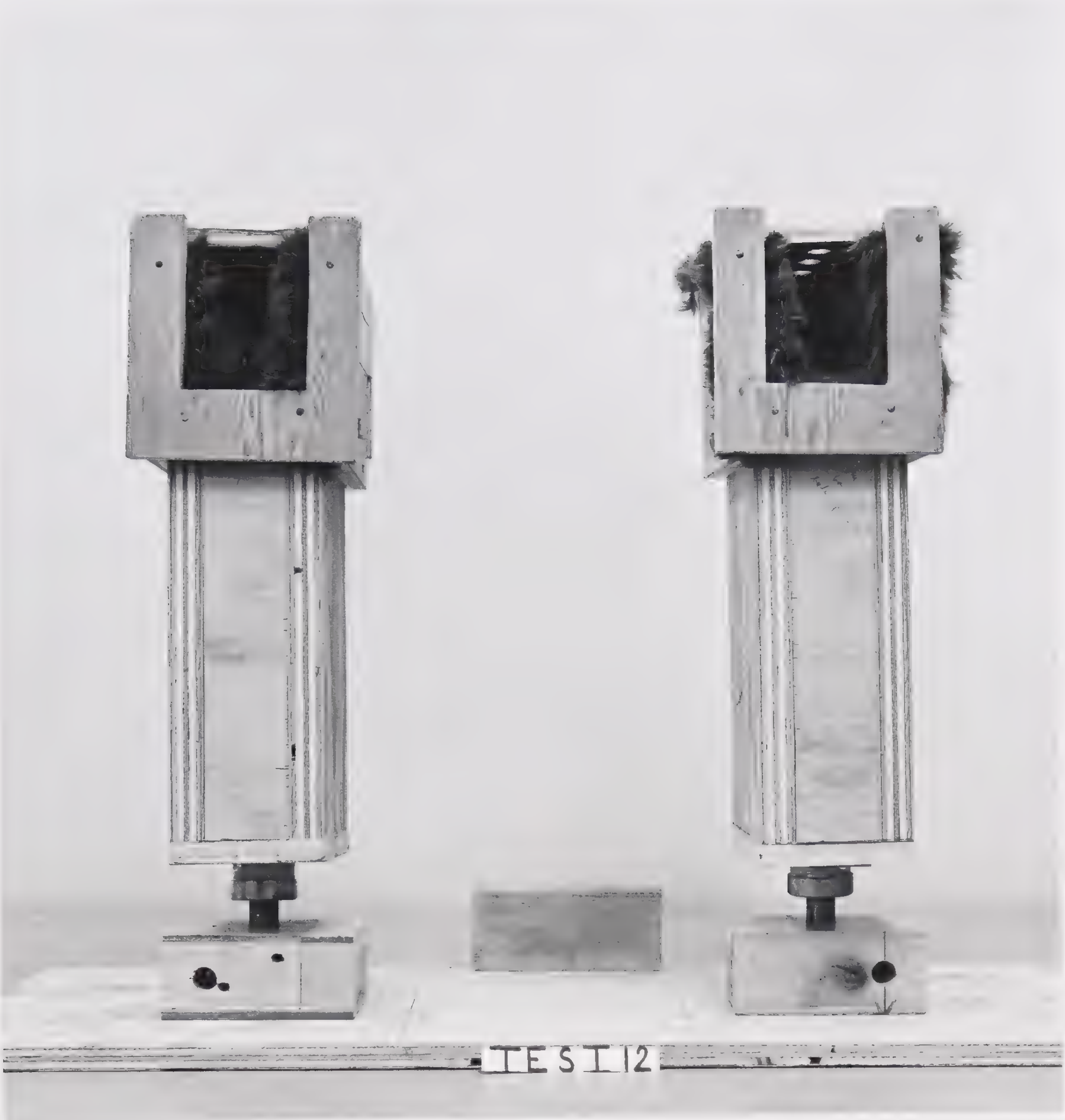

Figure 16: TEST 12 - Rotating Hairy Boxes

Figure 17: TEST 13 - Open Transparent Box

Test 15 - Block. Two food wells .5 inches deep and 12 inches apart center to center on the SPT could be covered by wooden blocks 3 inches by 3 inches by .5 inches thick. The well with the incentive was covered with one of the blocks. The blocks were fixed to the tray by short chains to facilitate retrieval.

Test 16 - Reach. Two food wells as described in Test 15 were on the SPT. The incentive was placed in one or the other well.

Test 17 - Elevated Reach. Two wooden pedestals 12.25 inches high, 12 inches apart center to center were placed on the SPT. The incentive was placed on one or the other pedestal.

The first pair of tests administered in Experiment III, Tests 6 and 7, were chosen to approximate Tests 2 and 3 of Experiment I. Test 6 was two latched boxes fixed to the SPT while Test 7 was two latched boxes suspended fairly freely. In other respects the two tests were the same. These tests were chosen because it was felt that opening the latch and obtaining the incentive would involve fine manipulations while pulling the box down into reach for Test 7 would involve coarser manipulations. Test 8 was designed partially as a control for the depth of the box but also with the idea of seeing what effect chaining of responses had on operating the latches.

Test 9 was designed in an attempt to control for visual cues as an influence in obtaining the incentive.

Tests 10 and 11 were designed similar to Tests 6 and 7 with the addition of a latch similar to that in Test 8 but with guards around the latches to ensure that each latch was opened separately.

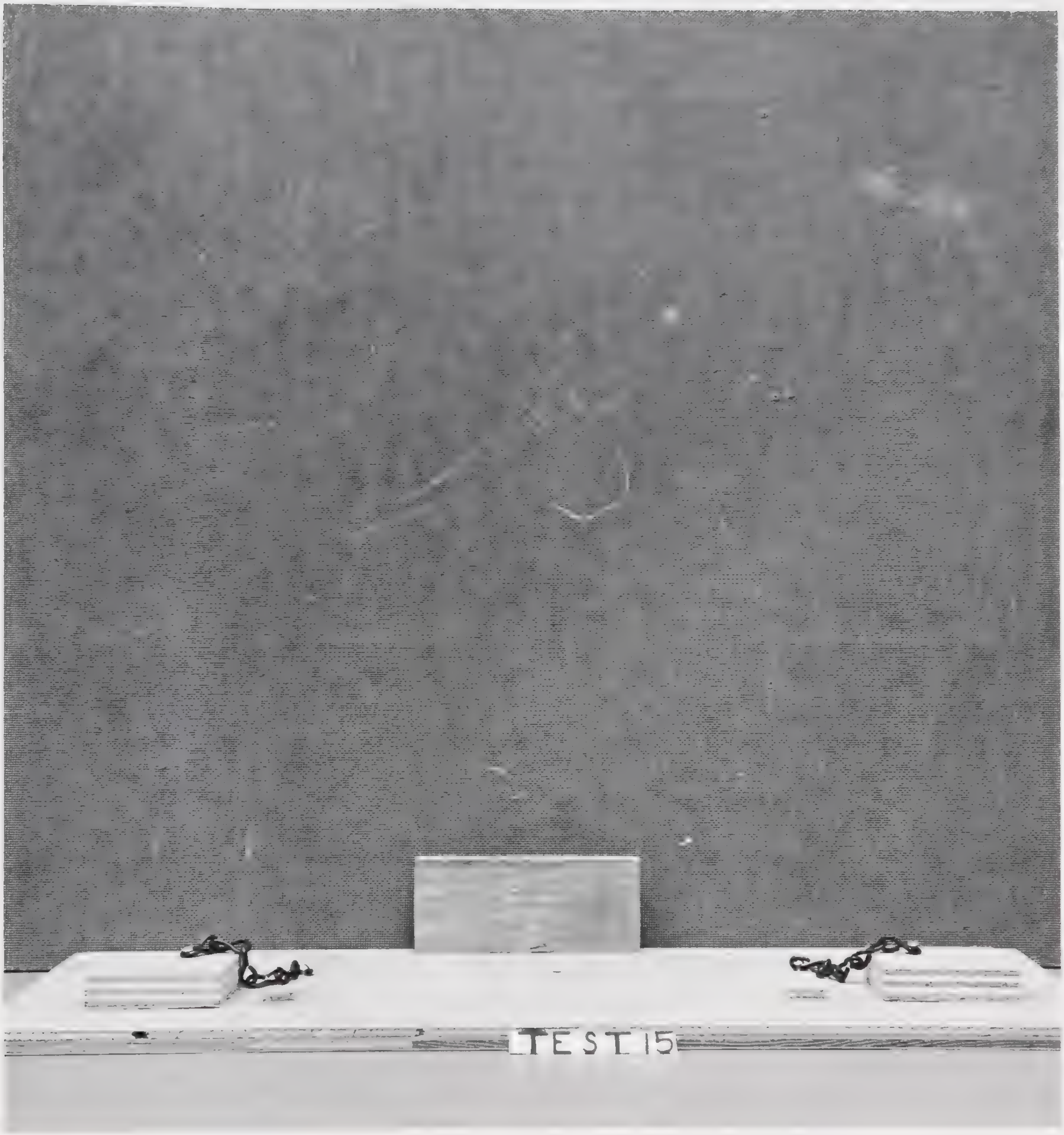

Figure 18: TEST 15 - Block

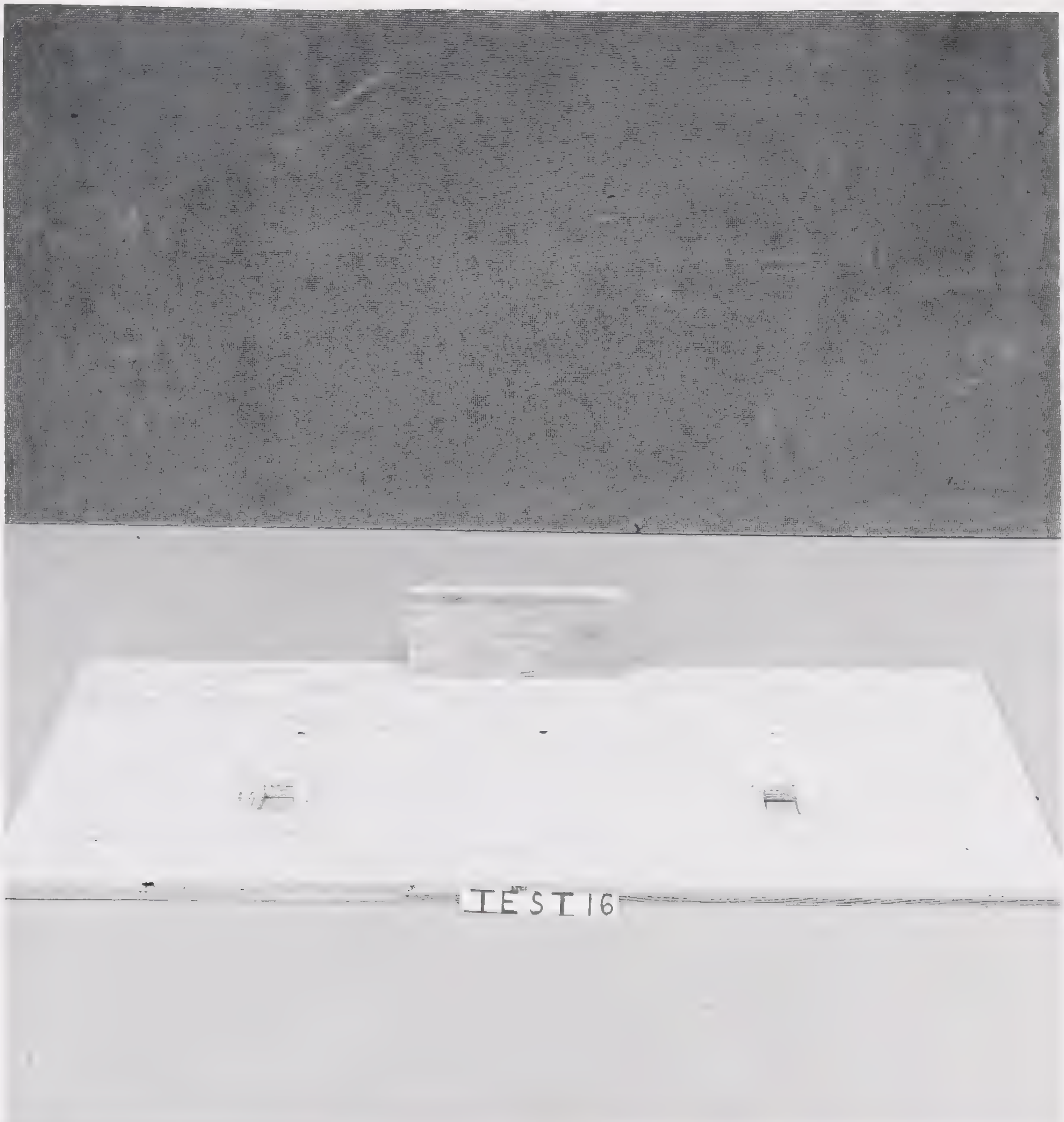

Figure 19: TEST 16 - Reach

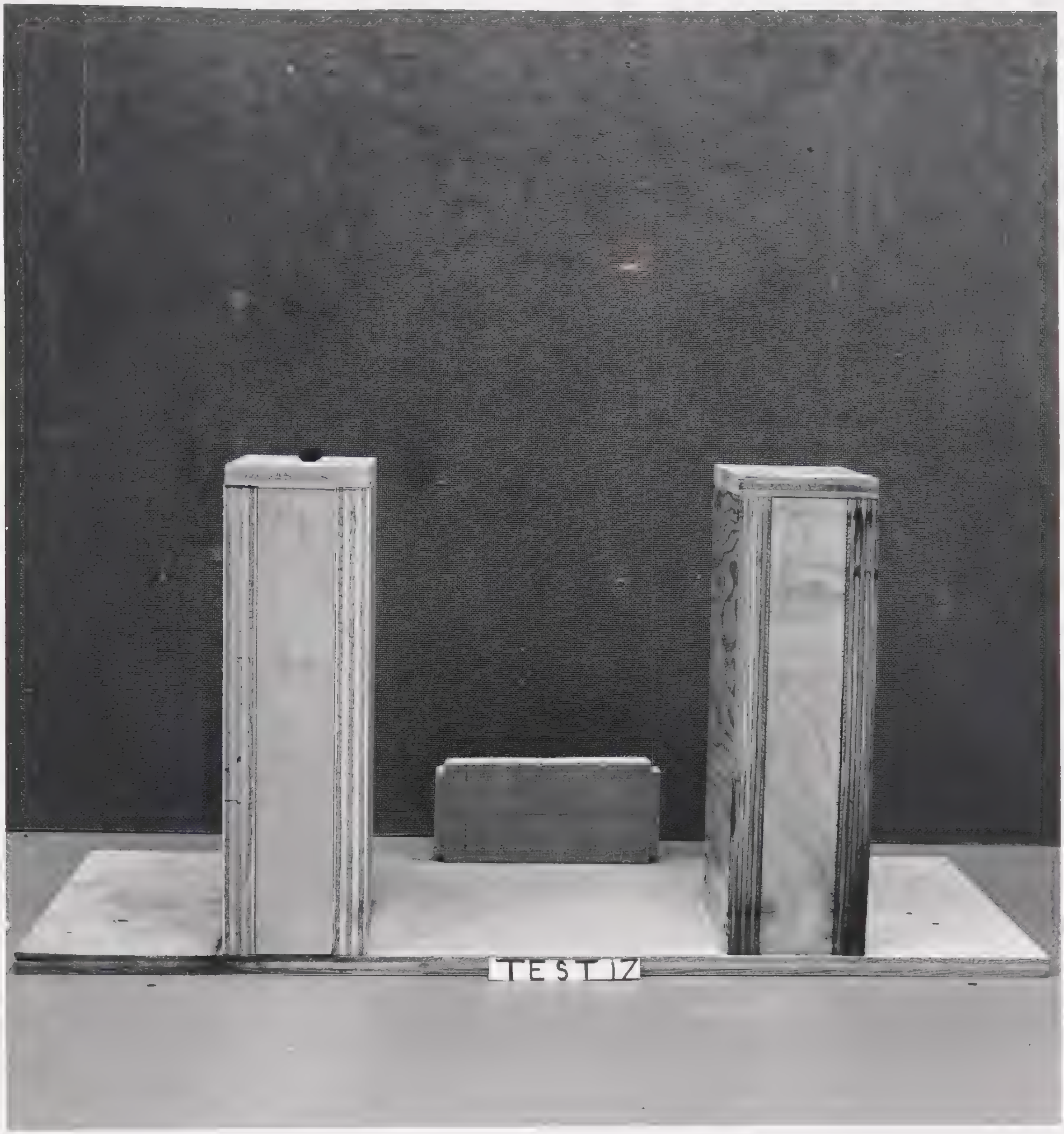

Figure 20: TEST 17 - Elevated Reach

Test 12 was designed partially with Test 4 in mind (the test which approximated grooming) and partially with the idea of producing a coarser manipulatory response of pulling the manipulanda around.

Tests 13 and 14 were designed to control for the depth of the boxes combined with opening the latches.

Tests 15 and 16 were designed to be like tests reported in the literature, ie. Test 15 was designed to be like Warren's Block Test (Warren, 1958); while Test 16 was designed like most Reach Tests (Brookshire and Warren, 1962; Warren, 1958). Test 17 was designed as a control for the height of the pedestals of Tests 1, 2 and 3.

Procedure

The basic procedure was as described in Experiments I and II. A synopsis of the testing received by the S's for Experiments I, II and III is given in Table 8 along with a synopsis of the responses recorded. All responses were recorded as the forepaw used, then transformed either to deviation scores or percentage left forepaw use. Each test in Experiment III had one session of 60 trials; retests were administered on Tests 10, 11 and 12.

Table 8: Synopsis of testing and responses recorded.

TEST	WEEKS	RETEST WEEK	RESPONSES
	Experiment 1		
1. Open trough	1 - 2	27 - 28	I
2. Fixed cylinder	1 - 2		I
3. Hanging cylinder	1 - 2	27 - 28	I
	Experiment 2		
4. Brush	4		M,I
5. Drawer pull	4		M,I
	Experiment 3		
6. Latch box	24		M_1,I
7. Hanging latch box	24		M_1,M_2,I
8. Two latch box shallow bottom	31		M_1,M_2,I
9. Opaque box	28		I
10. Inlaid two latch box	30	32	M_1,M_2,I
11. Hanging inlaid two latch box	30	32	M_1,M_2,M_3,I
12. Rotating hairy boxes	31	32	M,I
13. Open transparent box	32		I
14. Open box shallow bottom	32		I
15. Block	32		M,I
16. Reach	33		I
17. Elevated reach	33		I

I = hand used to obtain the incentive,

M = hand used to manipulate (M_1 - first manipulation, M_2 - second manipulation, M_3 - third manipulation)

RESULTS

Degree of Deviation as a Function of a Test. In accordance with the reasons given in Experiments I and II the data for Experiment III were transformed to a deviation score as a percentage. The transformed data is presented in Table 9. Significant forepaw deviation on a test is defined as a deviation in the use of one forepaw by $\pm 3\delta\%$ from chance performance, where $\delta\% = \sqrt{Npq} \times \frac{100}{N}$ and N = the number of trials, p=q=1/2, the probability of right and left responses, assuming no preference. The transformed data was examined using a criteria of a deviation of +3δ% from chance. Scores reaching criterion are significant beyond the .01 level (Table 10).

Figure 21 is a graph of the IQR's and medians of the deviation scores for the test measures. Some measures of Tests 7, 10, 11 and 12 are examples of tests producing strong deviations.

Table 10 indicates significant differences in the deviation scores between tests for the incentive measures (Wilcoxon match-pairs signed-ranks test, Siegel, 1967). The tests from Experiments I and II are included. Asterisks in the columns indicate which test measures are greater than row measures. For example the I measure of Test 11 is significantly greater than sixteen other I measures and only significantly less than one other measure. On the other hand, the I measure of Test 1 is not significantly greater than any other I measures but is significantly less than nine others. From Table 10 and Figure 21 it is apparent that usually those I measures with short IQR's and high medians (Test 3, Retest 3, Test 7, Test 11, Retest 11)

TEST

Monkey	6 M	6 I	7 M_1	7 M_2	7 I	8 M_1	8 M_2	8 I	9 I	10 M_1	10 M_2
1	90.0*	89.2*	93.3*	97.5*	98.3*	96.7*	93.3*	100*	96.7*	96.7*	100*
2	56.7	80.8*	79.2*	99.2*	100*	81.7*	95.0*	90.0*	81.7*	100*	100*
3	75.0*	75.0*	97.5*	85.8*	99.2*	98.3*	98.3*	80.0*	53.3	100*	100*
4	87.5*	93.3*	73.3*	82.5*	90.8*	85.0*	75.0*	95.0*	56.7	98.3*	100*
5	67.5*	55.8	98.3*	99.2*	96.7*	55.0	58.3	50.0	96.7*	100*	100*
6	64.2*	50.8	50.8	86.7*	96.7*	88.3*	91.7*	86.7*	80.0*	100*	100*
7	91.7*	64.2*	70.0*	92.5*	94.2*	73.3*	73.3*	61.7	71.7*	53.3	95.0*
8	78.3*	99.2*	95.0*	84.2*	100*	66.7	71.7*	98.3*	71.7*	93.3*	100*
9	63.3	68.3*	55.8	98.3*	84.2*	58.3	56.7	53.3	91.7*	95.0*	98.3*
10	85.8*	63.3	65.0	97.5*	98.3*	88.3*	95.0*	78.3*	78.3*	100*	100*
N	120	120	120	120	120	60	60	60	60	60	60
$\pm 3\delta$ %	13.7	13.7	13.7	13.7	13.7	19.4	19.4	19.4	19.4	19.4	19.4

* $p < 0.01$

Table 9: Deveation score (percentage) on test measures for individual monkeys.

TEST

10	Retest 10			11	11	11	11	Retest 11				12
I	M_1	M_2	I	M_1	M_2	M_3	I	M_1	M_2	M_3	I	M
53.3	85.0*	100*	71.7*	98.3*	100*	100*	100*	73.3*	55.0	60.0	100*	93.3*
53.3	95.0*	100*	76.7*	66.7	100*	100*	88.3*	95.0*	100*	100*	98.3*	96.7*
96.7*	80.0*	96.7*	71.7*	98.3*	100*	100*	100*	73.3*	53.0	100*	85.0*	96.7*
100*	100*	100*	100*	76.7*	96.7*	100*	100*	81.7*	100*	100*	100*	96.7*
95.0*	100*	100*	71.7*	100*	100*	100*	98.3*	93.3*	98.3*	100*	93.3*	100*
85.0*	51.7	100*	76.7*	98.3*	98.3*	100*	100*	85.0*	51.7*	51.7*	96.7*	88.3*
98.3*	96.7*	100*	96.7*	96.7*	93.3*	78.3*	100*	100*	98.3*	98.3*	100*	100*
98.3*	100*	100*	86.7*	98.3*	91.7*	90.0*	100*	75.0*	100*	100*	100*	88.3*
76.7*	100*	100*	93.3*	53.3	100*	100*	100*	98.3*	100*	100*	71.7*	76.7*
85.0*	100*	98.3*	96.7*	98.3*	100*	100*	100*	75.0*	80.0*	96.7*	100*	93.3*
60	60	60	60	60	60	60	60	60	60	60	60	60
19.4	19.4	19.4	19.4	19.4	19.4	19.4	19.4	19.4	19.4	19.4	19.4	19.4

Table 9: Continued.

TEST

12	Retest 12		13	14	15	15	16	17
I	M	I	I	I	M	I	I	I
100*	100*	100*	78.3*	91.7*	100*	100*	96.7*	91.7*
98.3*	100*	98.3*	93.3*	51.7	95.0*	61.7	85.0*	73.3*
86.7*	96.7*	81.7*	71.7*	61.7	70.0*	70.0*	91.7*	100*
98.3*	100*	100*	96.7*	51.7	58.3	71.7*	76.7*	55.0
100*	75.0*	100*	100*	58.3	53.3	53.3	53.3	56.7
96.7*	71.7*	98.3*	86.7*	53.3	100*	100*	100*	71.6*
98.3*	73.3*	58.3	70.0*	50.0	63.7	61.7	53.3	68.3
90.0*	90.0*	70.0*	96.7*	56.7	93.3*	90.0*	60.0	58.3
96.7*	85.0*	93.3*	88.4*	53.3	86.7*	73.3*	88.3*	51.7
100*	71.7*	96.7*	98.3*	71.7*	100*	98.3*	98.3*	73.3*
60	60	60	60	60	60	60	60	60
19.4	19.4	19.4	19.4	19.4	19.4	19.4	19.4	19.4

Table 9: Continued.

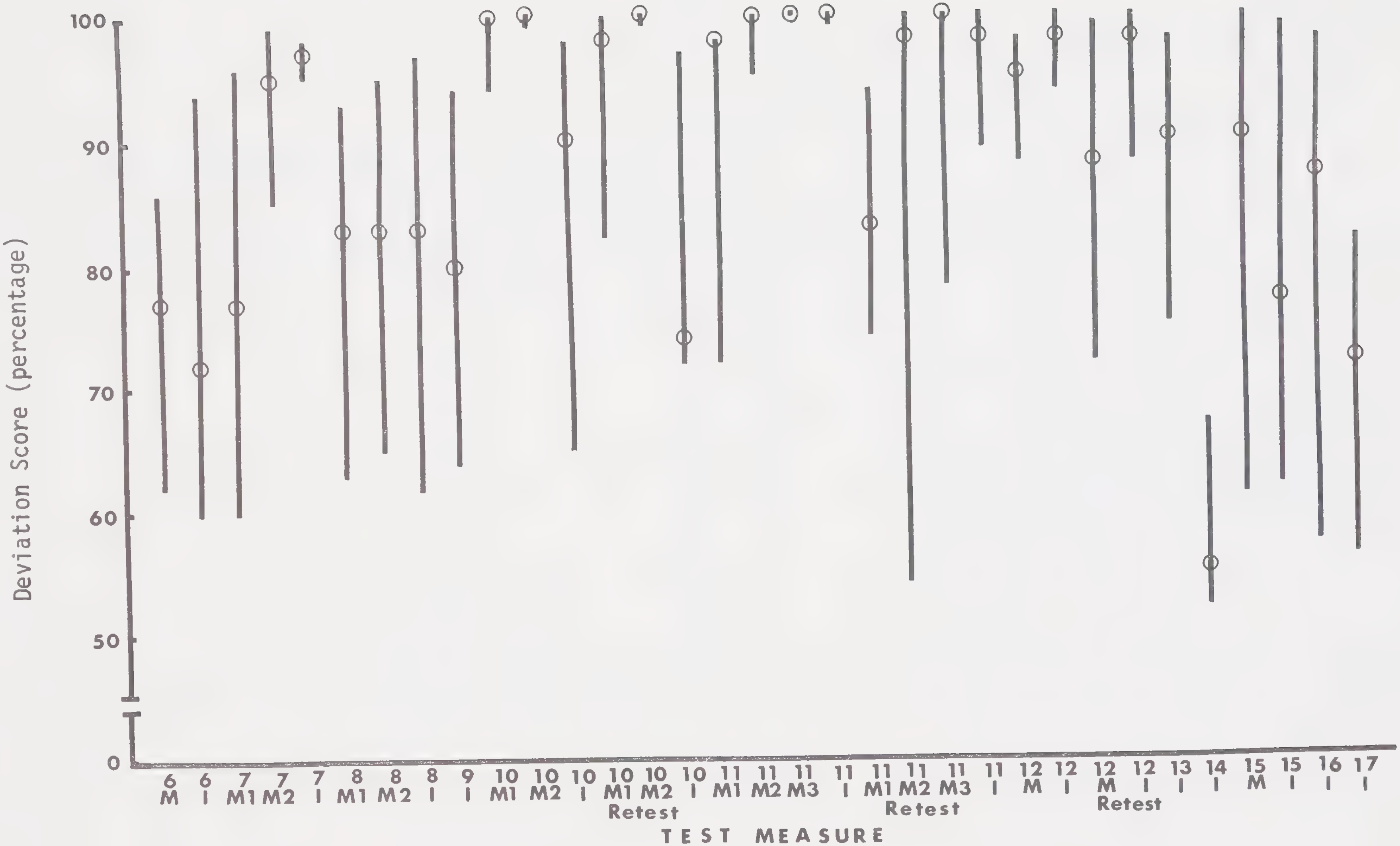

Figure 21: Interquartile Range and Median Deviation Score on Test Measures

Table 10: Wilcoxon test comparison of deviation scores on all incentive measures.

TEST	1	R 1	2	3	R 3	4	5	6	7	8	9	10	R 10	11	R 11	12	R 12	13	14	15	16	17	B
1				**	**				**		**		**	**	**	**	**						9
Retest 1				*	**				**	*	*		*	**	**	**	**					**	11
2				**	**		*		**		**		**	**	**	**	**	**		*	*		13
3																							0
Retest 3														*									1
4				**	**				**					**	*	*	*						7
5				*	*				**					**	**	*							6
6					*				**					**	**								4
7																							0
8				*					*					**	**								4
9					*				**					*			*						4
10									*					**									2
Retest 10																							0
11													**										1
Retest 11																							0
12														*									1
Retest 12														*									1
13					**										**		**						3
14				**	*				**	**	**	*		**	*	**		**		**	*	*	13
15				*					*					**									3
16					*				*					*	**		*						5
17				**					**				**	**		*							5
A	0	0	0	9	10	0	1	0	13	2	4	1	5	16	10	7	7	2	0	2	2	2	

* $p < 0.05$

** $p < 0.01$

R = Retest

A = total number of times that the column measure produces significantly greater deviations than the other measures

B = total number of times that the row measure produces significantly smaller deviations than the other measures

Test Measure	4M	5M	6M	$7M_1$	$7M_2$	$8M_1$	$8M_2$	$10M_1$	$10M_2$	Retest 10 M_1	Retest 10 M_2	$11M_1$	$11M_2$	$11M_3$	Retest 11 M_1	Retest 11 M_2	Retest 11 M_3	12M	Retest 12M	15M	B
4M					*			*	**				**								4
5M					*				**			*	**	*	*			*			7
6M					**				**			*	**	**	*			**			7
$7M_1$					*			*	**				**	**				*	*		7
$7M_2$									**				**								2
$8M_1$								*	**				**	**				*			5
$8M_2$								*	**				**	**				*			5
$10M_1$																					0
$10M_2$										**											1
Retest $10M_1$											*										1
Retest $10M_2$																					0
$11M_1$								*			**										2
$11M_2$									*												1
$11M_3$																					0
Retest $11M_1$									**		**		*								3
Retest $11M_2$											**										1
Retest $11M_3$																					0
12M									*		*										2
Retest 12M									*		*										2
15M									*		*		*	*							4
A	0	0	0	0	4	0	0	5	12	1	7	2	9	6	2	0	0	5	1	0	

* $p < 0.05$

** $p < 0.01$

A = total number of times that the column measure produces significantly greater deviations than the other measures

B = total number of times that the row measure produces significantly smaller deviations than the other measures

Table 11: Wilcoxon test comparison of deviation scores on manipulation measures.

are significantly greater than many of the other measures while they are not significantly less than many measures.

Table 11 contains a similar comparison for the manipulation measures. The same general trend as described above holds for the manipulation measures.

Spearman rank-order correlations on the deviation scores of both the incentive and manipulation data for all tests including those of Experiments I and II demonstrated that there was not a tendency for the monkeys to be consistently high or low deviators. There were few significant correlations, almost a chance number, and there was no pattern to the significant correlations.

Laterality preference as a function of a test. Table 12 contains the data from the test measures as the percentage of left responses. Significant forepaw preference was defined as in the previous two experiments i.e. ±38%; the data in Table 12 was examined using this criterion. The number of Ss with significant lefts and the number of Ss with significant rights on each measure are included at the bottom of the table and the number of significant lefts and rights for individual Ss are recorded to the right of the table.

For most of the I measures the number of Ss demonstrating significant use of the left forepaw is greater than the number of Ss displaying significant use of the right forepaw. Those tests in which the left is not used more frequently, except for test 10, are the tests which were not designed to specifically involve complex manipulations (Tests 13, 14, 15, 16 and 17). On the M measures

TEST	6	6	7	7	7	8	8	8	9	10	10
Monkey	M	I	M_1	M_2	I	M_1	M_2	I	I	M_1	M_2
1	10.0*	89.2*	6.7*	2.5*	98.3*	96.7*	93.3*	100*	96.7*	3.3*	0*
2	43.3	80.8*	79.2*	0.8*	100*	18.3*	5.0*	10.0*	81.7*	0*	0*
3	25.0*	75.0*	97.5*	14.2*	99.2*	1.7*	1.7*	20.0*	53.3	0*	0*
4	12.5*	98.3*	26.7*	82.5*	90.8*	15.0*	75.0*	95.0*	56.7	98.3*	100*
5	32.5*	44.2	1.7*	99.2*	3.3*	55.0	53.3	50.0*	96.7*	100*	100*
6	35.8*	50.8	49.2	13.3*	96.7*	11.7*	8.3*	13.3*	80.0*	0*	0*
7	8.3*	64.2*	30.0*	75.0*	94.2*	26.7*	26.7*	61.7	71.7*	53.3	5.0*
8	21.7*	99.2*	5.0*	84.2*	100*	66.7	41.7	98.3*	71.7*	93.3*	100*
9	36.7	31.7*	55.8	98.3*	15.8*	41.7	43.3	53.3	8.3*	5.0*	98.3*
10	14.2*	55.8	35.0	2.5*	98.3*	11.7*	5.0*	78.3*	78.3*	0*	0*
Significant Preferences											
R	8	1	5	5	2	6	5	3	1	6	6
L	0	6	2	5	8	1	2	4	7	3	4

* $p < 0.01$

Table 12: Percentage left forepaw responses by individual monkeys.

TEST

10	Retest 10			11	11	11	11	Retest 11				12
I	M_1	M_2	I	M_1	M_2	M_3	I	M_1	M_2	M_3	I	M
46.7	96.7*	100*	28.3*	98.3*	0*	0*	100*	73.3*	55.0	40.0	100*	93.3*
53.3	85.0*	0*	23.3*	66.7	0*	0*	11.7*	95.0*	0*	0*	1.7*	96.7*
3.3*	5.0*	0*	28.3*	98.3*	0*	0*	100*	73.3*	46.7	100*	85.0*	96.7*
100*	20.0*	96.7*	100*	23.3*	96.7*	100*	100*	81.7*	100*	100*	100*	3.3*
95.0*	100*	100*	71.7*	0*	100*	100*	98.3*	6.7*	1.7*	0*	93.3*	0*
15.0*	0*	0*	23.3*	98.3*	1.7*	0*	100*	85.0*	51.7	51.7	96.7*	88.3*
1.7*	51.7	0*	3.3*	3.3*	93.3*	78.3*	0*	100*	98.3*	98.3*	0*	100*
98.3*	96.7*	100*	13.3*	98.3*	91.7*	90.0*	100*	25.0*	100*	100*	100*	11.7*
23.3*	0*	0*	6.7*	53.3	100*	100*	0*	98.3*	0*	0*	23.3*	23.3*
85.0*	0*	98.3*	96.7*	98.3*	0*	0*	100*	25.0*	80.0*	96.7*	100*	6.7*
4	5	5	7	3	5	5	3	3	3	3	3	5
4	4	5	3	5	5	5	7	7	4	5	7	5

Table 12: Continued.

TEST

12	Retest 12		13	14	15	15	16	17	Significant Preferences	
I	M	I	I	I	M	I	I	I	R	L
100*	100*	100*	21.7*	90.0*	100*	100*	96.7*	91.7*	9	21
98.3*	0*	1.7*	6.7*	48.3	95.0*	61.7	15.0*	73.3*	18	10
13.3*	3.3*	81.7*	71.7*	61.7	30.0*	20.0*	8.3*	0*	19	11
98.3*	0*	100*	96.7*	51.7	41.7	28.3*	23.3*	45.0	9	20
100*	25.0*	100*	100*	41.7	53.3	46.7	46.7	43.3	9	15
3.3*	28.3*	1.7*	13.3*	46.7	0*	0*	0*	28.4*	20	7
98.3*	26.7*	100*	70.0*	50.0	38.3	38.3	53.3	68.3	12	13
90.0*	90.0*	41.7	96.7*	43.3	6.7*	10.0*	60.0	58.3	7	20
96.7*	85.0*	70.0*	12.6*	46.7	13.3*	26.7*	11.7*	48.3	16	8
100*	28.3*	93.3*	98.3*	71.7*	100*	98.3*	98.3*	73.3*	12	19
2	7	2	4	0	4	5	5	2	131	
8	3	7	6	2	3	2	2	3		144

Table 12: Continued.

significant use of the right forepaw is more frequent than significant use of the left forepaw.

Spearman rank-order correlations (Seigel, 1967) were done on the laterality scores for the measures of all the tests presented in this series of experiments. Only 10 correlations out of 136 were significant at the .05 level. Because by chance alone about 7 would be expected this indicates that there is not a consistent laterality preference (within Ss) for obtaining the incentive. However, Spearman rank-order correlations on the laterality scores of the manipulation measures of the tests did indicate a pattern of laterality preference (Table 13). One common feature of those tasks producing significant correlations is the involvement of latch opening.

Table 14 contains Spearman rank-order correlation on the Test-Retest measures. The pattern of significance suggests that one common underlying feature is the simultaneous use of the forepaws (Test 3, 11 and 12). Also the later component of sequential responses produce higher retest reliability (Test 10 M_2, Test 11 M_2, M_3 and I).

Table 15 contains Spearman rank-order correlations of the manipulation measures with the incentive measures within individual tests. Of the 21 possible correlations, 2 are significant beyond the .001 level, 1 beyond the .01 level and 2 beyond the .05 level. There is a slight tendency for negative correlations between the I and M measures to occur on those tests involving the latch but this is not marked. The negative correlations on Test 4 and 5 indicate that

Test Measure	5M	6M	$7M_1$	$7M_2$	$8M_1$	$8M_2$	$10M_1$	$10M_2$	Retest 10 M_1	Retest 10 M_2	$11M_1$	$11M_2$	$11M_3$	Retest 11 M_1	Retest 11 M_2	Retest 11 M_3	12M	Retest 12M	15M
4M	-.310	-.042	.358	-.736*	-.663*	-.511	-.569	-.570	.409	.291	.343	-.558	-.406	.498	.664*	.278	.152	-.108	.371
5M		.627	.658*	-.085	-.537	-.543	-.564	-.414	-.085	0	.175	-.079	-.092	.358	-.236	-.342	-.104	-.068	0
6M			.479	-.176	-.176	-.419	-.306	-.111	-.391	.212	.175	.069	.079	.394	-.391	-.161	.055	-.385	-.298
$7M_1$				-.365	-.693*	-.790†	-.782†	-.636	-.161	.394	.239	-.414	-.315	.176	.167	.003	.571	.567	-.170
$7M_2$					.235	.344	.693*	.796†	.376	.525	-.590	.818†	.815†	-.298	.271	-.151	-.573	.387	-.524
$8M_1$						.771†	.590	.454	-.157	-.058	-.071	.367	.487	.358	-.044	.075	-.146	.142	.143
$8M_2$							.734*	.598	-.305	-.035	-.175	.453	.592	.214	-.135	-.202	-.418	.296	.076
$10M_1$								.940 §	.362	-.062	-.680*	.806†	.893§	-.143	.442	.503	-.533	.630	-.072
$10M_2$									.202	-.166	-.608	.848†	.950§	.244	.202	.307	-.598	.474	-.270
Retest $10M_1$										.420	.415	.424	.443	.284	.796†	.608	-.548	-.003	.394
Retest $10M_2$											.310	.327	-.166	.467	.420	-.262	-.178	-.118	.587
$11M_1$												-.756*	-.476	.624	.415	.248	.194	.072	-.058
$11M_2$													.923§	-.141	.572	.285	-.478	.718*	-.378
$11M_3$														-.305	.443	.614	-.342	.712*	-.118
Retest $11M_1$															.294	-.055	-.343	-.409	.525
Retest $11M_2$																.703*	.323	.274	.165
Retest $11M_3$																	-.269	.246	-.028
12M																		.362	-.092
Retest 12M																			-.010

* $p < .05$
† $p < .01$
§ $p < .001$

Table 13: Correlation matrix for laterality scores on manipulation measures.

Test / Retest	1 I	3 I	10 M_1	10 M_2	10 I	11 M_1	11 M_2	11 M_3	11 I	12 M	12 I
1 I	.499										
3 I		.978§									
10 M_1			.572								
10 M_2				.736*							
10 I					.547						
11 M_1						.386					
11 M_2							.732*				
11 M_3								.907§			
11 I									.959§		
12 M										.439	
12 I											.870÷

* p<.05
† p<.01
§ p<.001

Table 14: Test - retest correlation matrix on laterality scores.

Incentive	Manipulation Measures M 1	M 2	M 3
4 I	-.709*		
5 I	-.985§		
6 I	-.430		
7 I	.303	-.569	
8 I	.535	.736*	
10 I	.506	.570	
Retest 10 I	-.418	-.556	
11 I	.504	-.475	-.185
Retest 11 I	.318	-.856†	-.488
12 I	-.296		
Retest 12 I	.185		
15 I	.973§		

* $p < .05$
† $p < .01$
§ $p < .001$

Table 15: Correlations of laterality scores for I and M measures within a test.

these tasks are bimanual while the positive correlation on Test 15 indicates that it is not.

Table 16 contains the significant left and right laterality preferences on the I and M measures for all tests as a percentage of the total possible. Although there is not a significant difference in the proportion of right responses on the I and M measures or the left responses on the same measures, examination of Table 16 indicates that left preference is associated with I measures while right preference is associated with M measures.

Individual Subjects: Table 17 contains the percentage distribution of the significant left and right laterality preferences for individual Ss on the I and M measures. Examination of Table 17 demonstrates that Ss 1, 4, 5, 8 and 10 display predominantly left responses on the I measures; however, on the M measures these Ss show about equal frequencies of significant left and right responses. Ss 2, 3, 6 and 9 display more significant right responses than significant left responses. For Ss 2 and 3 the M measures are largely responsible for this bias; for S 6 both the I and the M measures are responsible while for S 9 the I measures are largely responsible for the right bias. S 7 demonstrates about equal left and right preferences with the I measures biased slightly left and the M measures biased slightly right. Table 18 presents a summary of these results. A difference of 25% or greater in the percentage of significant preferences on a measure was considered to be a strong preference. Overall preference was determined by the difference in the total percentage for significant preferences.

	Right	Left
Incentive	26	48
Manipulation	50	36

Table 16: The distribution of significant right and left laterality scores on the I and M measures as percentage of total possible score.

	SUBJECTS																			
	1		2		3		4		5		6		7		8		9		10	
	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L
I	9	68	40	27	36	32	18	59	9	55	45	23	32	36	9	59	50	23	0	86
M	45	45	55	30	70	25	45	50	50	35	55	20	50	35	35	55	35	35	60	35
Total	26	57	48	29	52	29	31	55	29	45	50	21	40	36	21	57	43	29	29	62

Table 17: The percentage distribution of significant right and left laterality scores on the I and M measures for individual subjects.

Monkey	Incentive	Manipulation	Overall
1	L	-	L
2	r	R	r
3	r	R	r
4	l	l	l
5	L	r	l
6	r	R	R
7	l	r	-
8	L	r	L
9	R	-	r
10	L	R	L

L = strong left preference R = strong right preference
l = weak left preference r = weak right preference

Table 18: Summary of individual preferences.

Discussion

Degree of Deviation as a Function of a Test

Experiment III was an exploratory investigation of the effects that chaining of responses and simultaneous use of both forepaws necessitated by moveable manipulanda had on the production of deviations in preferential use of forepaws. Intuitively the combination of these features on an individual test should produce the more complex tasks and this is the interpretation of complexity that was utilized.

The importance of the simultaneous use of both forepaws for producing strong deviations on the I measures can be deduced from a study of Table 10: strongest deviations were produced on Test 7, 11 and 12, which all involved moveable manipulanda. It should be noted that Test 3, Experiment I (Hanging Cylinder) also produced strong deviations on the I measure. Test 5, Experiment II, although involving moveable manipulanda, did not produce strong I measure deviations. A possible explanation for this discrepancy is that the manipulanda moved in only one plane while for the other tasks they could move in many planes.

A comparison of the results obtained from Tests 7 and 11 on the one hand, with those from Tests 6 and 10 on the other emphasizes the importance of the simultaneous use of forepaws in producing strong deviations on I measures. The only difference between the two sets of tests is that the former involve the use of moveable manipulanda, whereas the latter do not.

A positive effect of chaining of responses on the production

of strong deviations could not be readily demonstrated from the results of the present series of tests. There appears to be no correlation between the number of M measures (Table 8) and the production of strong deviations on I or M measures (Tables 10, 11).

Generally, the hypothesis that those tasks defined as more complex in this experiment would produce the stronger deviations is upheld. This is an agreement with the results of other experiments (Cole, 1957; Kounin, 1938; Warren, 1958).

Laterality Preference as a Function of the Test

In Experiment II it was suggested that the two types of grip described by Napier (1956, 1960) as precision and power were associated with preferential use of forepaws. Although Experiment III set out with the intent of examining this distinction great difficulty arose in determining which type of grip was being utilized. Because of this difficulty the experiment focused on task complexity and the gross separation of manipulative responses into I and M.

The results indicate that in general there was a distinction between these two measures (I and M), (Table 16). There was a bias on the I measures toward left preferences and a bias on the M measures toward right preferences. However, some individual Ss demonstrated reversals in this trend.

The low intratest correlations between the I and the M measures indicate that the manipulation measures did not determine which forepaw was used for the incentive measure on that test. In Experiment III only one M measure of Retest 11 was significantly negatively correlated

with the I measure for that test. This lack of negative correlations indicates that the two measures (I and M) are relatively independent.

Within tasks with multiple M responses there was consistency of performance. There were significant positive correlations between the M measures of Tests 8, 10 and 11 especially those involving opening the hasps. Comparisons between tests indicate that the I measures were not well correlated with each other while there was a pattern of significant correlations on those M measures that involved the hasp. This demonstrates that performance on the M tasks that are similar in structure is more consistent than performance on the I measures.

The results are interpreted as weak support for the hypothesis that one forepaw would be associated with the M measure while the other forepaw would be associated with the I measure. The trend demonstrated in the results was toward the left forepaw on the Incentive measures and toward the right forepaw on the Manipulation measures.

<u>Individual Subjects</u>

The distribution of laterality preferences of individual monkeys is comparable to distributions reported in the literature (Brookshire and Warren, 1962; Cole, 1957; Kounin, 1938). There appears to be a relatively continuous distribution of individual laterality preferences from strong left to strong right. However, the present experiment has attempted to investigate the effect that task characteristics have on the production of laterality preferences. In general, there was a trend toward a larger number of significant left preferences on the incentive measures and a larger number of

significant right preferences on the M measures. Looking at individual Ss, though, only one S (S 10) displays this pattern of preference (ie. stronger L on I, stronger R on M). The rest display a bias only on one characteristic, a bias in the same direction on both characteristics or no bias on either characteristic.

Similar inconsistencies between general trends and individual S performance have been reported previously in the literature (Brookshire and Warren, 1962; Ettlinger, Blakemore, and Milner, 1968; Ettlinger and Moffett, 1964). The dependent variables of I and M produce an interesting statistical group trend but appear to be of questionable value as predictors of individual S performance.

General Discussion

It seems intuitively reasonable that the more difficult tasks should produce stronger preferences; however, this has been questioned (Brookshire and Warren, 1962). The present series of experiments supports the hypothesis that difficult tasks do produce stronger preferences although a problem arises about the definition of difficulty. For this series of experiments, judgements by the experimenter were the basis for determining difficulty or complexity. Two features, simultaneous use of both forepaws and chaining of responses were considered in judging the complexity of a test.

If difficulty had been defined as the fine manipulations necessary to obtain an incentive from a confined space then, for Experiment I, the expected result would have been high preferences on both the Fixed Cylinder (Test 2) and the Hanging Cylinder (Test 3). However, these two tests did not produce comparable preferences. Thus from Experiment I it became apparent that the coordinated involvement of both forepaws was relevant for defining difficulty because Test 3 involved the use of both forepaws simultaneously, while Test 2 involved only one forepaw: Test 3 produced the stronger preferences.

The relevancy of this feature for the definition of difficulty was upheld in Experiment II and, in addition, an extension to this feature became apparent. Test 5 (Drawer Pull) involved the use of both forepaws simultaneously and like Test 3 involved a moveable manipulanda but it did not produce preferences as strong as those on Test 3. Closer examination of the tests revealed that in Test 5 the manipulanda could move in only one orientation, back and forth, while in Test 3 it

could move in almost any direction. Thus, freedom of movement of the manipulanda in conjunction with the simultaneous use of both forepaws was incorporated into the definition of difficulty.

Experiment III upheld the relevancy of the simultaneous use of both forepaws for the definition of difficulty but indicated that the second feature (chaining of responses) was probably not an important factor; those tests which involved a long chaining sequence did not necessarily produce stronger preferences. If the assumption is made that the experimental definition of difficulty is correct then the original hypothesis (i.e., that increased task complexity gives rise to stronger forepaw preferences) may be only partially correct. However tasks involving simultaneous use of both forepaws did produce stronger preferences; this does uphold the original hypothesis that the more complex tasks produce stronger preferences.

The results also support an hypothesis that preferences are differentiated by the characteristics of the responses performed. The I measures produced predominantly left responses and the M measures produced predominantly right responses. It is suggested in the discussion of Experiment II that the I and M measures may be examples of a precision (fine manipulation) - power (gross manipulation incorporative force) dichotomy. This dichotomy has been suggested by Napier, (1956, 1960, 1961) with respect to prehensile patterns of movement in primates. Because of the apparent similarities between the patterns of movement described by Napier (1956, 1960, 1961) and the patterns of movements utilized by the <u>S</u>s in responding to the tasks it seemed appropriate to make a distinction between the task measures which

correspond to the distinction made by Napier.

Semmes (1968) has made a distinction between the functional organization of the two hemispheres in man which can be interpreted as a functional basis for the distinction between precision and power grips by Napier (1956, 1960). She suggests that the left hemisphere in man is typified by focal or hierarchical organization of function, while the right hemisphere is diffusely organized. She also suggests that the differences in the hemispheres are the bases for distinct types of behavior and that each hemisphere is preferentially associated with separate types. She concluded that the right hemisphere is concerned with tactual and spatial factors while the left hemisphere is concerned with finer articulatory movements. Extending her suggestions to hand preferences, especially with respect to the precision-power dichotomy, it is possible, in man, that the left hemisphere is involved in precise manipulations while the right hemisphere is involved in the grosser ones.

In the present experiments, particular forepaw preferences were found to be associated with certain task characteristics and this preference was a trend across Ss. Left preference was predominantly associated with the response of obtaining the incentive while right preference was predominant on the manipulation measures (Table 16). Obtaining the incentive involved more spatial and tactual responses than did the manipulative responses, thus the right hemisphere in subhumans may be organized like the right hemisphere in humans. In addition, the results indicate that right forepaw preferences were associated with the manipulative measures. These measures involved

the chaining of responses and simultaneous use of both forepaws. Therefore, this type of hierarchical response pattern could be associated with the left hemisphere in subhumans as it may be in man.

In dealing with laterality preferences of individual Ss it is apparent that in general the preference shown on the Incentive measures is the overall preference of the S (Table 18).

Brookshire and Warren (1962) determined individual laterality preferences in 19 monkeys and described an apparently continuous distribution of preferences from strong left through ambidexterity to strong right. The results of the present series of experiments conform reasonably with this aspect of their results. Brookshire and Warren (1962) have also shown that monkeys display relatively consistent laterality preferences within successive administrations of the same test but few of these Ss show a generalized preference for the same forepaw over a series of dissimilar manipulatory tasks. Again, the results of this series of experiments are in agreement with their results. In addition, however, the present series of experiments demonstrated that individuals displayed consistent laterality preferences on similar M measures of separate tasks. This was demonstrated for those measures involving manipulation of the hasp.

Although there were overall trends towards biases on the M and I measures the results were not strong enough to conclude that a definite pattern of responses on these measures can be predicted for individual Ss. It may be said, however, that performance on the I measure appears to be a fairly good indication of the Ss overall laterality preference.

Suggestions for further study: The distinction between the precision and the power responses was not made clearly enough in the present series of experiments. In addition, a wider range of tests should be used; these should incorporate varying degrees of involvement of the moveable manipulanda, chaining of responses and simultaneous use of both forepaws combined with more tests which have widely different task characteristics within the precision or the power dimensions. These types of tests would measure the generality of the predominant preferences throughout each dimension. Without such investigations, interpretations of the results as supporting the conclusion that the hemispheres differ in functional organization will be somewhat weak.

In addition to the above suggestions, care should be taken to remove the confounding from carry-over effects. Because of the exploratory nature of the present experiments this was not done, but in light of the possibility of such an effect randomization of presentation of tests should alleviate this problem.

As an extension of this type of investigation which goes well beyond the scope of the present experiment, examination of cortical lesions and their effects on performance should be done. This would involve trying to distinguish between the left and right hemispheres with respect to functional organization.

REFERENCES

Baldwin, J.M. _Mental development in the child and the race_. (3rd ed. rev.) New York: Macmillan, 1906.

Baldwin, J.M. 'Dextrality', in _Baldwin's Dictionary of Philosophy and Psychology_. New York: Macmillan, 1911.

Ballard, P.B. Sinistrality and speech. _Journal of Experimental Pedagogy and Training College Record_, 1911, _1_, 298.

Brinton, D.G. Left-handedness in North American Aborigonal Art. _The American Anthropologist_, 1896, _9_, 175-181.

Brookshire, K.H. & Warren, J.M. The generality and consistency of handedness in monkeys. _Animal Behavior_, 1962, _10_, 222-227.

Burt, Sir Cyril. _The Backward Child_. London: University of London Press, 1961.

Cole, J. & Glees, P. Effects of small lesions in sensory cortex in trained monkeys. _Journal of Neurophysiology_, 1954, _17_, 1-13.

Cole, J. Laterality in the use of the hand, foot and eye in monkeys. _Journal of Comparative Physiological Psychology_, 1957, _50_, 296-299.

Cronholm, J.N., Grodsky, M., & Behar, I. Situational factors in the lateral preference of rhesus monkeys. _Journal of Genetic Psychology_, 1963, _103_, 167-174.

Cunningham, D.J. Right-handedness and left brainedness. _Royal Anthropological Institute of Great Britain and Ireland Journal_, 1902, _32_, 273-296.

Ettlinger, G. Lateral preferences in monkeys. _Behavior_, 1961, _17_, 275-287.

Ettlinger, G., Blakemore, C.B., & Milner, A.D. Opposite hand preferences in two sense modalities. _Nature_, Vol. 218, p. 1276, 1968.

Ettlinger, G., & Moffett, A. Lateral preference in monkeys. _Nature_, 1964, 204, 606.

Finch, G. Chimpanzee handedness. _Science_, 1941, _94_, 117-118.

Froude, J.A. _Thomas Carlyle in London, 1834-1881_, London: Longmans, Green and Co., Vol. 2, 1884.

Gautrin, D., & Ettlinger, G. Lateral preferences in the monkey. Cortex, 1970, 6, 287-292.

Gordon, H. Left-handedness and mirror writing. Brain, A Journal of Neurology, 1920, 43, 312-368.

Haefner, R. The educational significance of left-handedness. Teachers College Contributions to Education. 1929, 92-96.

Harlow, H.F., Settlage, P., & Grether, W. Handedness in monkeys. Unpublished studies at the University of Wisconsin Primate Laboratory, 1933, in Kounin, J.S. Laterality in monkeys. Journal of Genetic Psychology, 1938, 52, 375-393.

Hollis, W.A. Lopsided generations. Journal of Anatomy and Physiology, 1874, 9, 264-265.

Jolly, A. Prosimian's manipulation of simple object problems. Animal Behavior, 1964, 12, 560-570.

Kounin, J.S. Laterality in monkeys. Journal of Genetic Psychology, 1938, 52, 375-393.

Langkavel, H. Deutsche Revue 1902, 27, As cited by D.J. Cunningham, Right-handedness and left brainedness. Royal Anthropological Institute of Great Britain and Ireland Journal, 1902, 32, 273-296.

Martin, F. Bulletin of the Society of Anatomy, 1820, p. 42.

Milner, A.D. Distribution of hand preferences in monkeys. Neurophysiological, 1969, 7, 375-377.

Napier, J.R. The prehensile movement of the human hand. Journal of Bone and Joint Surgery, 1956, 38B, 902-913.

Napier, J.R. Studies of the hands of living primates. Proceedings of the Zoological Society London, 1960, 134, 647-657.

Napier, J.R., & Napier, P.H. A handbook of living primates: Morphology, ecology and behavior of nonhuman primates. London: Academic Press, 1967.

Ogle, W. On dextral pre-eminence. Medico-chirurgical Transactions, 1871, 36, 279-301.

Osawa, K. Uber Linkshandigkeit, In: Proceedings of Physiological Congress (Turin) 1901.

Pedro, M. The Treasurie of Ancient and Moderne Times. London: William Jaggard, 1613, p. 507.

Rife, J.M. Types of dextrality. Psychological Review, 1922, 29, 474-481.

Seigel, S. Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill, 1967.

Semmes, J. A non-tactual factor in astereognosis. Neuropsychologica, 1965, 3, 295-315.

Semmes, J. Hemispheric specialization: A possible clue to mechanism. Neuropsychologica, 6, 11-26.

Trevarthen, C.B. Manipulative strategic of baboons and the origins of cerebral asymmetry. In: Hemispheric Asymmetry of Function. M. Kinsbourne (Ed.). London: Tavistock, 1970.

Tsai, L., & Mauer, S. Right-handedness in white rats. Science, 1930, 72, 436-438.

Warren, J.M. Handedness in the rhesus monkey. Science, 1953, 118, 622-623.

Warren, J.M. The development of paw preferences in cats and monkeys. Journal of Genetic Psychology, 1958, 93, 229-236.

Warren, J.M., Abplanalp, J.M., & Warren, H.B. The development of handedness in cats and rhesus monkeys. In: Early behavior: Comparative and developmental approaches. H.W. Stevenson, E.H. Hess, & H.L. Rheingold (Eds.). New York: John Wiley and Sons, 1967, 73-101.

Wile, I.S. Handedness right and left. Boston: Lothrop, Lee and Shepard, 1934.

Wile, I.S. The relation of left-handedness to behavior disorders. American Journal of Orthopsychiatry, 1932, 2, 44-57.

Wilkin, S. Vulgar Errors, Works of Sir Thomas Browne. London: Henry G. Bohn, Vol. IV, 1852.

Wilson, Sir D. The right hand and left-handedness. Proceedings and Transactions of the Royal Society of Canada, 1886, Sec. 2.

Woo, T.L. Dextrality and sinistrality of hand and eye. Biometrika, 1928, 20, 79-148.

Woodruff, C.E. Expansion of Races. New York: Rebman & Co., 1909, p. 120.

Yashioka, J.G. Handedness in rats. Journal of Genetic Psychology, 1930, 38, 471 (a).

Yashioka, J.G. Handedness in rats. Psychological Bulletin, 1930, 27, 656-657.

Yerkes, R.M. Chimpanzees; A laboratory colony. New Haven: Yale University Press, 1943.